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CONTENTS

EDITOR'S NOTES

The contents of this volume are the results of some of the scientific reports presented at a colloquium on the ecology and taxonomy of African small mammals hosted by Carnegie Museum of Natural History from 19 to 22 September 1977. In all, forty-one persons who generally specialize in research on African small mammals responded to invitations and met during that period; some presented results of their research during formal morning sessions but, perhaps more importantly, all joined in afternoon discussions centered around an attempt to increase the international cooperation and coordination of research on a continental basis. Such an approach is becoming more important with the increasing cost of research, changing environments and destruction of some ecosystems, and political instability in Africa. Studies of medical zoology in Africa continue to point out the need for continent-wide studies of taxonomy and long-term studies of ecology of potential small mammal hosts of disease vector and reservoirs of causal organisms. Changing weather patterns with protracted droughts, and increasing population growth outstripping food supplies, make it necessary that as little of the resources as possible be lost to small mammal damages. Finally, there has been a tremendous upsurge in interest in African mammals on the part of conservationists, particularly regarding endangered species and the potential extinction of some gene pools.

The state of research on ecology and taxonomy of small mammals in Africa is a number of decades behind that of Europe and North America. The contents of this volume will amply indicate the differences in approach to solving the various problems and the general "state of the art" in this area of research. Only through cooperation and coordination of research efforts can the highest return be obtained.

Because of limited logistical support and facilities, the number of participants invited to this colloquium was kept low. If another is scheduled in the near future, perhaps wider participation among specialists will be possible.

Individual papers in this volume have been arranged in generally accepted phylogenetic order regardless of topic, beginning with elephant shrews and continuing through hyraxes. Near the end are the papers dealing with speciation and biogeography; these are followed by a review of published karyological data for African mammals. The final paper discusses problems and priorities of research on the taxonomy and ecology of African small mammals. From an editorial standpoint, an attempt was made to get as much uniformity of style as possible without significantly changing the context of the manuscripts.

The completion and publication of this volume would not have been possible without the unselfish support, cooperation, and encouragement of Hugh H. Genoways, Publications Editor, Carnegie Museum of Natural History. I am deeply indebted to him for all of this help. My thanks go also to Teresa M. Bona, Technical Assistant for Publications, who was helpful beyond the requirements of her job in retyping, editing, and checking of manuscripts, and in keeping records and addresses; Stephen L. Williams, Associate Editor, for working with the figures; and Nancy Perkins for enhancing some of the figures. My warmest thanks must go to the individual contributors for their cooperation and support in putting together this volume.

The colloquium which precipitated this volume would not have been possible without the active support of a number of people. Chief among these are the people who helped house and feed the participants and furnished transportation to the colloquium site. Suzanne Braun, Cathy H. Carter, Murray H. de la Fuente, Stefannie B. Elkins, Hugh H. Genoways, Joyce Genoways, Caroline A. Heppenstall, Mary Ann Jones, Thomas J. McIntyre, Suzanne McLaren, R. Laurie Robbins, Judith Schlitter, Pierre Swanepoel, Daniel F. Williams, and Stephen L. Williams all helped in many ways. Mary H. Clench, Albert O. and Gilbert O. Lenhart, and Dan Roslund worked hard to assure that the colloquium site was satisfactory. I want to thank William and Ingrid Rea and Graham and Jane Netting for offering sleeping quarters for a number of the participants. The Market Spot, Bud's Bakery, Valley Dairy, Goodman's Distributing Co., and William Downs, Penn State University Southwestern Regional Experimental Farm, helped assure that all were well fed. Ruth Scott and Martha Shope allowed us the use of various personal items of furniture. William Campbell, Carnegie Institute Cafeteria, was helpful in acquiring various items. Ann R. Nieser and Flora Gibson typed many invitations and proposals. I am grateful for the help and support of all of them.

A portion of the travel support of some of the participants from Africa was made possible by a grant from the Office of International Programs, National Science Foundation (INT77-08721).

Whatever success this colloquium enjoyed is directly related to the support of Craig C. Black, Director of Carnegie Museum of Natural History. Although the idea for such a colloquium was formulated in 1972, it was not possible to begin serious planning until 1976. At this time, Dr. Black pledged his support and helped make it financially possible to have such a colloquium and to publish a volume of proceedings resulting from it.

Finally, I want to thank Karl F. Koopman of the American Museum of Natural History, New York, for serving as Honorary Chairman. I am grateful that he would lend his support to the idea of a colloquium. During the colloquium he freely offered the stability and knowledge gained by his years of experience to insure that an atmosphere of professionalism was maintained throughout the meeting.

Duane A. Schlitter

EVOLUTION OF THE RUMP REGION IN THE GOLDEN-RUMPED ELEPHANT-SHREW

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ABSTRACT

Rhynchocyon chrysopygus has a distinct rump patch, which lies just above an area of exceptionally thick skin ("dermal shield"). The possible function(s) of these structures are discussed in relation to published hypotheses for the evolution of other mammalian rump patches and dermal shields. It is suggested that conspecific territorial aggression and diurnal predation have resulted in the two structures evolving both as a morphologically protective conspecific target organ and a pursuit invitation signal.

INTRODUCTION

The literature dealing with the function of mammalian rump patches not only contains several different hypotheses for their evolution, but also, in some cases, attempts to explain the occurrence of nearly all mammalian rump patches with one model (Smythe, 1970*a*; Guthrie, 1971). In this paper I will consider some of these hypotheses in terms of life-history data from an elephant-shrew (Macroscelidea), which suggests that some rump patches have evolved due to more than one selection process and serve multiple functions. In the development of the multifactor hypothesis, it should become clear that it is unrealistic to apply any one explanation for the evolution of rump patches to all mammalian taxa.

The golden-rumped elephant-shrew, *Rhynchocyon chrysopygus* Günther, is restricted to the open forests and woodlands of coastal Kenya north of Mombasa. It is the largest elephant-shrew species, weighing about 540 g and having a head-body length of about 280 mm (Fig. 1).

I began a 21-month field study of free-living *R. chrysopygus* at the Gedi Historical Monument (20 km south of Malindi) in April 1971. The 44-ha monument is covered with lowland, semi-deciduous forest with a 20-m high canopy. The forest floor is relatively open and covered with a carpet of dead leaf litter throughout the year (Fig. 2).

Animals were driven into fishing nets strung loosely along the ground. Each individual was fitted with a distinct combination of colored bird bands on its rear legs before being released. Behavior of marked animals was studied by systematically walking a trail grid through the forest.

RESULTS AND DISCUSSION

Life History

R. chrysopygus is diurnal, spending nearly 75% of the day slowly walking along the surface of the forest floor noisily probing for invertebrates with its long nose and forefeet (Fig. 2). It neither climbs nor burrows, but is capable of very swift cursorial locomotion. During the night it sleeps in a dry leaf nest on the forest floor. The individuals of monogamous pairs occupy equal, congruent territories (mean 1.7 ha) which they defend sex-specifically. Territorial defense involves linear chases, one animal running behind another, until the intruder is driven over a boundary. The long canine teeth of adults are probably associated with this aggression. Pair-bond behaviors are infrequent, yet the pair is stable over time, changing only when an individual disappears. The animals breed continuously throughout the year. Adult coloration is exhibited at birth by the single, precocial young weighing about 80 g. It is weaned when it first emerges from the nest, about 2 weeks after birth. It then follows its mother around for 2 or 3 days before becoming almost completely independent on the parental territory. There is no parent-young aggression and subsequent offspring may simultaneously occupy the parental territory.

Fig. 1.—Adult *Rhynchocyon chrysopygus*, illustrating the distinct golden rump patch.

The southern-banded harrier hawk (*Cicaetus fasciolatus*), black mamba (*Dendroaspis polylepis*), cobras (*Naja* spp.), and man are known predators. The elephant-shrew's reaction to potential predators is very similar to many ungulates (Eisenberg and Lockhart, 1972). It freezes at the first sign of danger, but if further disturbed, walks slowly away, loudly slapping its tail on the dead leaf litter; or it runs away in a gait that is like that of a stotting gazelle; or it flees at full speed, loudly hammering the leaf litter with its rear legs. In all cases it normally stops just within sight of the predator, and pauses until the latter makes another move. Then it either takes flight again or, after 5 to 15 min, silently disappears into the forest. If two or more individuals are disturbed, they flee in different directions. Once established on a territory, *R. chrysopygus* may live to be 3 or 4 years of age. The life history of this elephant-shrew is documented in more detail in my dissertation (1976) and monograph (in press).

During the behavioral work I collected monthly specimens for reproductive and diet studies. This material was taken from the nearby, structurally similar Arabuko-Sokoke Forest, in an area which was scheduled for clear-cut and burning. While preparing study skins from these specimens, differences in skin thickness were noticed. On several skins the subdermal muscles were carefully removed and then a grid was inked on the inner surface of the fresh, flat skins. Thickness was measured with a screw-gauge micrometer. Hair lengths were measured from randomly chosen hairs cut from the surface of study skins.

The Rump Patch

Both sexes have a distinct golden rump patch, which is only slightly erected when the animals are excited or stressed. There is no difference in the extent of rump patch coverage between the sexes. Rump hair is longer than hair on the middle of the back (means = 22.2 mm and 16.6 mm, respectively;

Fig. 2.—Predator's view of a foraging adult *Rhynchocyon chrysopygus* on the open, leaf-littered forest floor at Gedi Ruins.

20 specimens, 15 hairs each). The rump hair length of females is significantly longer than that of males (means = 23.0 mm and 21.4 mm, respectively; 10 specimens each, 15 hairs/specimen; $P < 0.001$, t-test). The 1.6 mm difference between the means is so small that it is doubtful whether it has any appreciable visual effect. This is especially true when considered in relation to the overlap between the range of mean rump hair lengths for the different individual female and male specimens (20.4 mm–27.2 mm and 19.1 mm–24.2 mm, respectively).

The Dermal Thickening

In both sexes the skin under the rump patch is thicker than on the middle of the back (Figs. 3 and 4). This is most pronounced in males. One normal adult male specimen had rump skin that was three times thicker than on the back. Histological examination of an adult male's rump skin shows that there are no unusual features except for its thickness (Fig. 5). Subadult animals do not show dermal thickening. It is probable that the shorter rump hair in males is a secondary effect of their thicker rump skin. If hair length could be measured from follicle tip to hair tip, there probably would be no significant difference in length between the sexes.

When all visible, small body scars from 84 study skins are cumulatively plotted on a skin-map, they all fall on or very near the rump patch (Fig. 6). Male skins have proportionally, but not significantly, more scars than females ($P < 0.5$, χ^2 test). I think the most likely explanation is that these scars result from canine wounds inflicted during intraspecific aggressive chases.

Sexual Dimorphism and Sex-Specific Behavior

The only externally visible sexual dimorphism is the much longer male canine tooth. Ten adult female and 10 adult male specimens had significantly different canine lengths (Table 1; see Ansell and Ansell, 1973, for a similar condition in *Rhynchocyon cirnei*).

There is evidence that males were more intensely

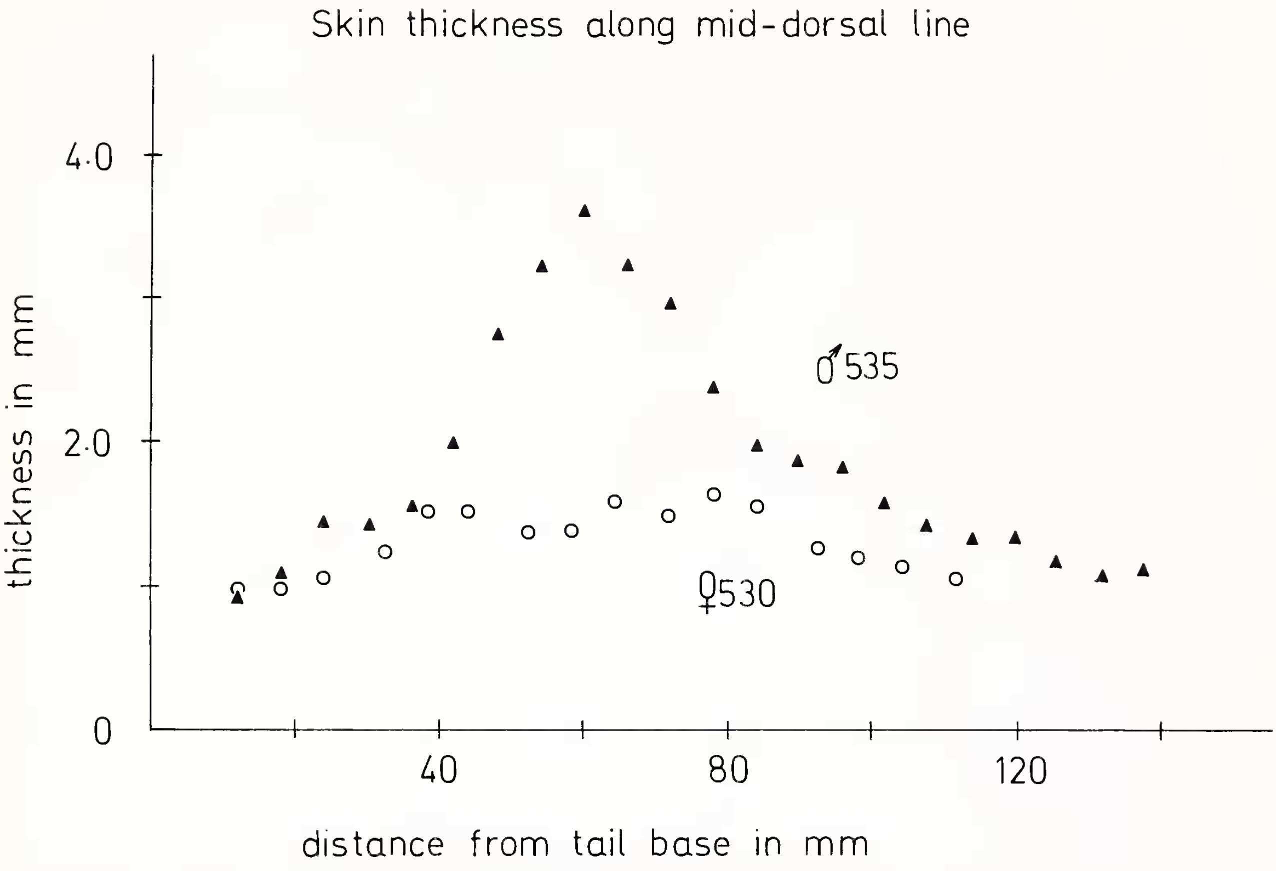

Fig. 3.—Skin thickness of an adult male and female *Rhynchocyon chrysopygus*.

territorial than females, for they scent marked, "violated" territorial boundaries, and were involved in interpair aggressive encounters more frequently than females (Table 1). Aggressive encounters were infrequent events, but in a 1 week period I saw the same two females chase one another many times, which is very unusual. These data contribute to the lack of significance between the levels of male and female aggression in Table 1.

Table 1.—*Sexual dimorphism and sex specific behaviors in* Rhynchocyon chrysopygus.

Trait	Female	Male	Chi-square on original data
Mean canine length	4.6 mm	6.6 mm	$P < .001$
Scent marking*	3.3%	9.7%	$P < .001$
Territorial violations*	3.1%	12.2%	$P < .001$
Interpair aggressive encounters*	1.0%	1.3%	$P < .5$

* % of total sightings.

Hypotheses for the Evolution of Dermal Thickening

If dermal thickenings function as protective shields from dense vegetation, as proposed by Dubost and Terrade (1970) in the chevrotain, *Hyemoschus aquaticus*, and in duikers, *Cephalophus* spp., then some substantial difference in behavior between the sexes would be expected to explain the sexually dimorphic thickening. This reasoning also applies to the idea that dermal thickenings may serve as a protective device against predators. No differences in behavior were observed that would support either of these two hypotheses for *R. chrysopygus*.

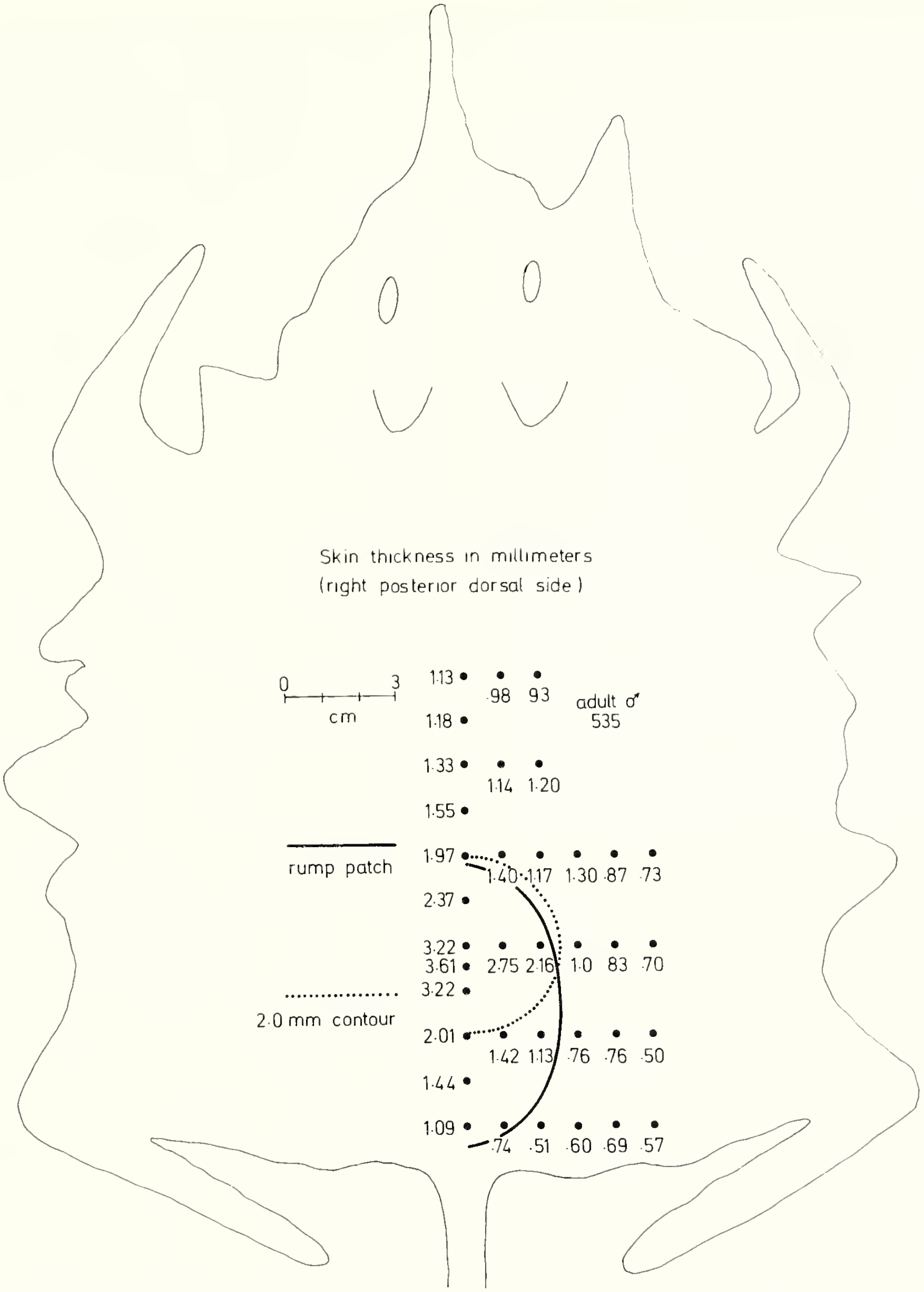

Fig. 4.—Skin thickness and rump patch location on an adult male *Rhynchocyon chrysopygus*. Solid-line arc represents rump patch margin, dotted-line arc the 2.0 mm thickness contour of the dermal shield.

It has been suggested that thick rump skin may serve, in some way, to erect the rump patch. The male rump patch does not appear any more or less erectile than the female's, and there is no histological evidence for such a mechanism in the skin (Fig. 5).

The mountain goat, *Oreamnos americanus*, is described by Geist (1967) as having a "dermal shield" where injury would most likely occur during conspecific fighting. Jarman (1972) found a similar structure in the territorial impala, *Aepyceros melampus*. Perhaps *R. chrysopygus* has evolved a

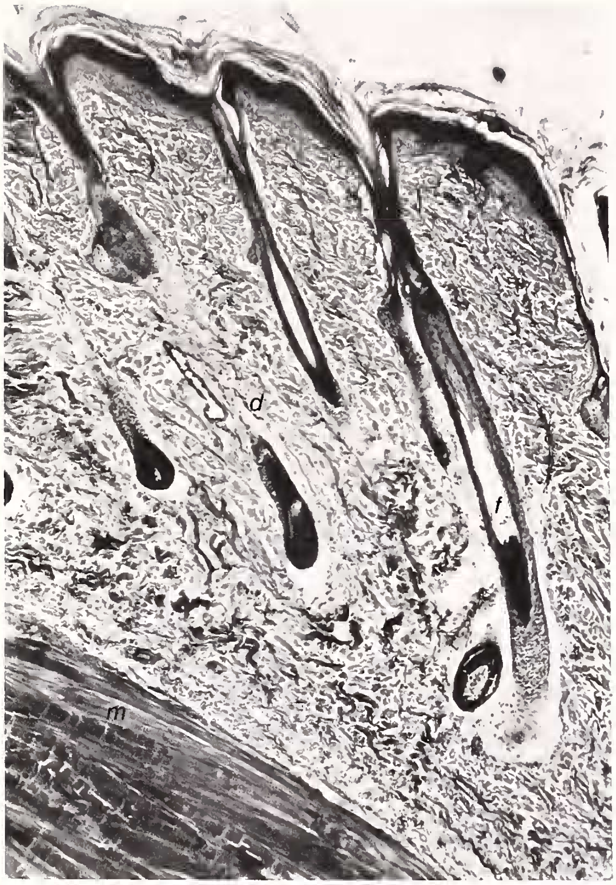

Fig. 5.—Longitudinal section of rump skin from an adult male *Rhynchocyon chrysopygus*. m = subdermal muscle. f = hair follicle. d = dermis.

dermal shield in response to territorial interpair aggression. This hypothesis is supported by the elephant-shrew's large canine tooth, fighting behavior, dermal shield location, cumulative scar pattern, and the thicker shield in the more intensely territorial male.

Hypotheses for the Evolution of the Rump Patch

Guthrie (1971), stimulated by Geist's ideas (1971) on mountain sheep (*Ovis canadensis*), proposed that mammalian rump patches evolved as intraspecific appeasement or submission signals. These signals function by changing a dominant animal's aggression to a sexual behavior due to the rump region's association with copulatory displays. Guthrie (1971) also suggests that other rump patch functions may be secondarily derived from the original submission/appeasement function. Kleiman (1974) suggests that the various rump displays in the hystricomorph rodents have secondarily evolved different functions from the original sexual function. I never observed any specific elephant-shrew rump patch display behavior that would support Guthrie's ideas for *R. chrysopygus*. In this elephant-shrew, the process of redirecting aggressive behaviors to sexual behaviors by a rump patch display would presumably not function in female-female encounters because a rump display would not stimulate a female sexually. This would result in only males evolving the rump patch, which is not the case in *R. chrysopygus*.

It has been suggested that a rump patch may increase the golden-rumped elephant-shrew's crypsis in the patchily-lighted, dry-leaf littered forest floor. It is my experience that the animals are not visually or behaviorally camouflaged. Their dark bodies contrast greatly with the light rump patch and leaf litter (Fig. 2), and the elephant-shrew's fleeing behavior does not indicate that it is relying on crypsis as a defense mechanism against detection by potential predators.

There is little evidence to support the hypothesis that *R. chrysopygus*'s golden rump functions as an intraspecific predator warning signal, as proposed for the rump patch of fallow deer, *Dama dama* (Alvarez et al., 1976). *R. chrysopygus* pairs were only rarely within visual contact of each other (less than 20% of my sightings) and because the rump patch is not highly erectile, there is no distinct on/off mechanism, which would be necessary if it were to function in this manner. There is some evidence that the tail slapping and rear-leg hammering behaviors can serve as warning signals (Rathbun, in press).

It has been suggested that the elephant-shrew's rump patch is a visual cohesive signal between the newly emergent young and a parent, helping to maintain a close distance between a pair while they forage. This function would be the visual equivalent of the auditory stridulating organ in the tenrec (*Hemicentetes semispinosus*; Eisenberg and Gould, 1970). The juvenile cohesive signal function is not consistent with the lack of a father-juvenile bond and the presence of a rump patch in male *R. chrysopygus*.

Hirth and McCullough (1977) present data to support an antipredator cohesive signal function for the tail-flagging display of the white-tailed deer, *Odocoileus virginianus*. In this case, the individuals of the prey species benefit by a coordinated flight from

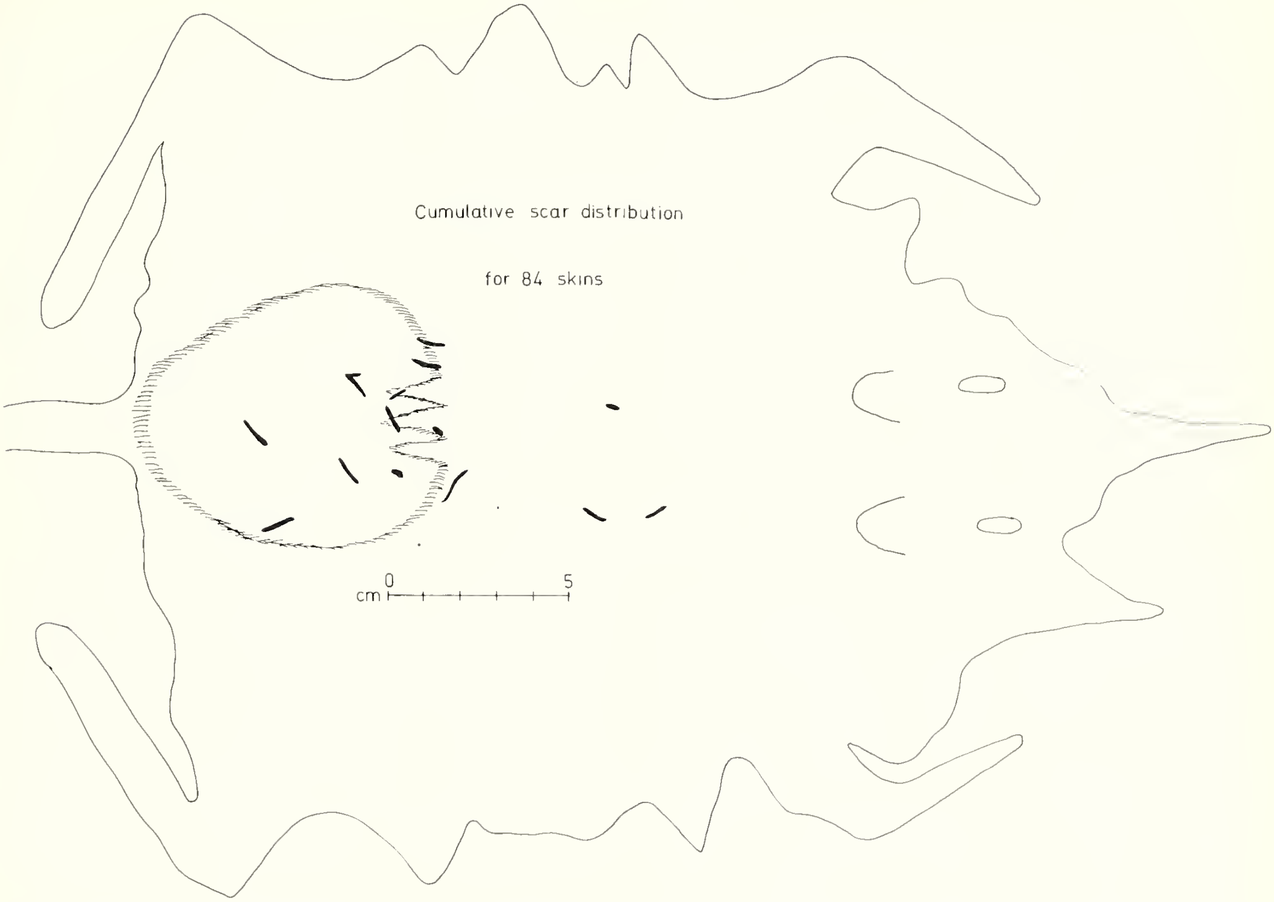

Fig. 6.—Location of 13 dermal scars (five female and eight male) from 43 female and 41 male *Rhynchocyon chrysopygus* study skins.

a predator, which is signalled by the rump display. The dispersed nature of the elephant-shrews, together with their flight in different directions when disturbed, does not support the antipredator cohesive signal function for the golden rump of *R. chrysopygus*.

Smythe (1970*a*, 1977) suggests that rump patches may serve as predator "pursuit invitation signals." By stimulating a predator to attack prematurely, a healthy individual is able to flee successfully and the location and intent of the predator are revealed, thereby reducing the danger of ambush. Smythe (1970*a*) suggests that stotting-like gaits and rump patch displays are used to invite pursuit. *R. chrysopygus* is probably frequently preyed upon by the harrier hawk, which hunts visually by perching 2 to 4 m above the relatively open forest floor waiting for an opportunity to make a quick, concealed ambush (Rathbun, in press). This is precisely the type of predation needed for visual invitation signals to evolve. The structure of the Kenyan coastal forest results in direct-line visibility being restricted to about 10 m, which is conducive to the evolution of auditory invitation signals. I believe the golden-rumped elephant-shrew's rump patch and behavioral complex of stotting, rear leg hammering, tail slapping, and short, obvious flight followed by a pause, are directed toward diurnal bird and mammal predators in an attempt to attract their attention and induce their exposure and/or premature attack, as proposed by Smythe (1970*a*, 1977).

The three allopatric species of *Rhynchocyon* occupy similar habitats, and except for distinctly different body coloration, their morphology is very similar (Corbet and Hanks, 1968). Kingdon (1974) has suggested several explanations for the variation in color. He thinks the checkered back and rump of *R. cirnei* may be an adaptation for camouflage, whereas the difference between *Rhynchocyon petersi*, with its pure black back and rump, and *R. chrysopygus* may be related to differences in sexual behavior which evolved as an "ethological barrier." More information is needed on the ecology and behavior of the *Rhynchocyon* species in order to verify these ideas.

I have discussed briefly some hypotheses which might conceivably explain the evolution of the dermal shield and the rump patch in *R. chrysopygus* as though the two structures were unrelated in this animal. The dermal shield lies directly beneath the rump patch (Fig. 4) and I feel that there is probably an integrated function in the two structures. The rump patch may serve as a conspecific target organ, attracting the blows of a pursuing elephant-shrew to a region of the body, which is not only relatively immune to serious injury, but also morphologically adapted to receive the blows. This is a similar mechanism to the "deflective marks" extensively described by Cott (1940), where a predator is attracted to a less vital part of the body by a very distinctive coloration or marking. In the case of the elephant-shrew, the predator is a conspecific individual defending its territory through aggression and the distinctive mark is the golden rump.

CONCLUSIONS

I think the data for *R. chrysopygus* support a multifactor explanation for the evolution of its rump patch. The location of the dermal shield, the scarring pattern, and the aggressive behavior indicate that the rump patch, with its very distinctive coloration, may serve as a conspecific target organ. On the other hand, because there is no significant sexual dimorphism in the rump patch corresponding with the rump skin, this suggests that the patch may have an additional, even distinct, function. The elephant-shrew's attention-gathering behavior while fleeing a potential predator, and its distinct rump patch, support Smythe's predator pursuit invitation hypothesis (1970*a*, 1977). Predator selection pressure probably acts equally on both sexes, resulting in the male and female rump patches being equal in size. Thus two distinct selection pressures, conspecific territorial aggression and diurnal predation, are probably involved in the evolution of the rump patch in *R. chrysopygus*.

It is unlikely that the dual rump patch function proposed for the elephant-shrew can be used as a general model for mammalian rump patch evolution. It is inappropriate to try to apply models developed for relatively social animals, such as many of the larger ungulates (Hirth and McCullough, 1977), to less social species. It would, however, be interesting to compare mammals that have similar life histories, such as *R. chrysopygus* and an agouti, *Dasyprocta*. The latter inhabit South American forests, and, like *R. chrysopygus*, are diurnal, cursorial, territorial, probably monogamous, and some bear a distinct rump patch (Morris, 1962; Smythe, 1970*b*). The yellow-back duiker, *Cephalophus silvicultor*, may also be comparable to *R. chrysopygus*.

If the rump patch functions proposed above for the golden-rumped elephant-shrew are valid, and Geist (1971), Alvarez et al. (1976), and Hirth and McCullough (1977) are correct in their interpretation of rump patch function in the species that they consider, it would not only seem fairly certain that rump patches have evolved independently several times within the Mammalia (Guthrie, 1971), but probably also due to several different selection pressures.

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REVIEW OF DRINKING BEHAVIOR OF AFRICAN FRUIT BATS (MAMMALIA: MEGACHIROPTERA)

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ABSTRACT

Certain captive African Megachiroptera drink regularly from a hanging posture. There are very few reports of these animals drinking in the wild, nearly all claiming that they would drink by skimming over open water surfaces and scooping water or wetting their fur and licking water from this afterward. This paper summarizes and critically deals with the literature on the subject, and presents some new evidence suggesting that the skimming maneuvers of some fruit bats might serve a purpose other than drinking. The discussion includes some related observations on Australasian Megachiroptera.

INTRODUCTION

Little has been written about possible drinking habits of African Megachiroptera in the wild. About fruit bats in general Novick (*in* Novick and Leen, 1969) wrote: "Fruit bats like the flying foxes and their smaller relatives rarely drink water, apparently they derive all the water they need from their moist food." Rosevear (1965) stated about West African fruit bats that "the demand of the body for water must be satisfied . . . to a considerable extent by the intake of liquified fruit pulp or floral nectar." Indeed one might expect that these animals, whose diet probably consists mainly of juicy fruits and equally water-rich nectar, would not need to drink water too. There are reports however which suggest that at least some wild fruit bats do drink. Two ways of drinking have been described, the first for captive animals and the second for animals in the wild. Quite a few species of Megachiroptera have been kept in captivity, but hardly any author paid attention to whether or not his animals drank. Notwithstanding discussions of their diet, it may not even be stated if water was offered (for example, Blackwell, 1966, 1967; Brosset, 1966*a*; Coe, 1976; Jones, 1972; Lawrence and Novick, 1963).

DRINKING RECORDS

Kulzer (1958, 1969) related how his captive *Rousettus aegyptiacus* (Geoffroy, 1810) and *Eidolon helvum* (Kerr, 1792) drank water from bowls, rapidly with their tongues, in a dog-like manner. *Rousettus* came down to the cage floor to drink, but *Eidolon* preferred to remain hanging. This is most probably related to the ability of *Rousettus aegyptiacus* to take flight from an even surface without effort, as I have observed in the zoo in Amsterdam where a small number of unknown provenance is kept (1977), and the apparent lack of this ability in *Eidolon* (Kulzer, 1968). At Windhoek, Namibia, Dr. C. G. Coetzee kept a crippled specimen of *Eidolon helvum*, which drank regularly from a bowl (personal communication, 20 September 1977.) Brosset (1966*b*) observed wild *Eidolon helvum*, probably in northeast Gabon, drinking from the sap of palm trees, which had been collected by Africans for the production of palm wine. As far as I know this is the only record of wild African Megachiroptera drinking in a manner more or less comparable to that observed by Kulzer (1958, 1969) in his captive specimens.

The other manner of drinking described for some Megachiroptera is to skim close to the surface of water and, in some way or other, take in water. In 1841, Prof. J. A. Wahlberg observed unidentified fruit bats near Port Natal (=Durban), South Africa, drinking in this way (Petermann, 1858). Rousselot (1950) related how he saw *Eidolon helvum* and *Epomophorus gambianus* (Ogilby, 1835) flying so close to the surface of a river that they could wet their ventral fur from which they would lick the water afterward. He observed *Eidolon* doing so at Ségou in Mali, and observed *Epomophorus gambianus* both at Ségou and at Maradi in Niger but does not state where he saw this species perform in this manner. Rosevear (1965) suggested that insectivorous bats would exhibit this behavior much more often than fruit bats would, but does not seem to have observed fruit bats drinking in this way himself. Novick (*in* Novick and Leen, 1969) mentioned the habit for insectivorous bats but, as appears from the above quotation, remained equally vague about fruit bats on this point. The ornithologist Mr. Roy Parker, at the time Curator of the Zoology Museum of the University of Ibadan, Nigeria, told me that he had often seen how *Eidolon helvum* came down at dusk to the water of the swimming pool of the Staff Members Club on the campus of the university. He believed the animals to be drinking (personal communication, August 1976). Dr. M. El Rayah saw *Eidolon helvum* skimming over the water of the Nile at Khartoum in Sudan, but did not observe further details (personal communication, 20 September 1977). At Makokou, northeast Gabon, Mr. J. Bradbury kept *Hypsignathus monstrosus* Allen, 1861, in captivity in a large enclosure with a large bowl of water on the floor. This bat regularly drank by scooping water with its mouth while flying low over the bowl (Dr. P. Charles-Dominique, personal communication, 20 September 1977).

PADDLING BATS

When traveling through Nigeria in the summer of 1976 I stayed for 2 weeks in Pandam Wildlife Park, a small game reserve just north of the village of Pandam (9°15′N, 7°50′E) that includes the 2 square mile Lake Pandam. There I enjoyed the hospitality of the zoologists Chris Smeenk and his wife Nellie, who told me of their observations of *Eidolon helvum* skimming over the lake. According to them, *Eidolon* did not drink when close to the water surface but touched it with its legs. On 7 July 1976, the three of us made a canoe trip on the lake for a more detailed study of this phenomenon. At twilight, from approximately 1840 to 1920 h, hundreds of *Eidolon* approached the lake, all coming from the southwest and eventually continuing roughly to the northeast. Only a few bats continued their flight without interruption. Most of them, when they had reached open water (much of the lake was covered with water lilies), came down to it in one circular movement (infrequently two or three circles were described). Then they flew parallel with and very close to the water surface for a short time and at a certain moment dipped their hind legs into the water. This dipping lasted much less than a second. Thereafter they flew up and continued on their way. A striking detail was the apparent hesitation, which most bats showed in their movements before dipping. We observed several individuals, who at the last moment refrained from dipping and continued on their way without having dipped. However, we also saw a small number of bats who dipped more than one time. These continued flying low over the water after their first dip, and dipped up to four times. On one occasion I counted five dips. These repeated dips followed shortly upon one another, reminding one of a well flinched drake-stone. After that these bats also resumed their flight, undoubtedly towards their feeding grounds.

The bats flew in small groups of a few dozens or less, arriving at different times during about 40 min, and all these groups displayed the described behavior. This enabled us to focus on new individuals and observe this behavior many times. Nevertheless, it was very hard to establish what was actually happening. The bats kept considerable distance, apparently avoiding our presence. It proved moreover very difficult to observe correctly what was happening at the division of air and water, and of course our sight was hindered by the gradual fading of light.

Later I heard of a possibly similar observation. The zoologist Rob Robelus told me that he had watched large bats skimming over the water of a swimming pool at Bébédjia near Moundou, in southwest Tchad, in September 1969. These bats touched the water with some part of their ventral side, but were not believed to be drinking (Dr. R. A. Robelus, personal communication, July 1977).

DISCUSSION AND CONCLUSIONS

The more conventional and seemingly more likely way of drinking as described for certain African Megachiroptera, that is, lapping while in a hanging or clinging position, has been observed in the wild only once (Brosset, 1966*b*). Because in this case, the bats (*Eidolon helvum*) drank no water but the probably tasty sap of a palm tree, the question remains whether they were hunger- or thirst-induced. The habit shown by captive *Rousettus aegyptiacus* and *Eidolon helvum* of drinking water regularly does not necessarily reflect natural behavior. Their demand for water may well have been brought about by a shortage of liquid in the food offered. Kulzer (1958, 1969) gave his *Rousettus* bananas, apples, and oatmeal porridge, and his *Eidolon* bananas and figs. In this respect, it is possibly of significance that his *Rousettus* always drank immediately upon feeding (Kulzer, 1958). On the other hand, *Rousettus aegypticus* in the Amsterdam zoo, which are given a much more varied diet with juicier fruits, also drink regularly (Mr. F. Gangel, personal communication, August 1977). The fact that wild African Megachiroptera drink regularly, and in a similar manner, is still to be proven.

The other manner of drinking water, by scooping or lapping it directly while skimming close to the water surface or indirectly by wetting the fur while skimming over the water and licking water from the fur afterward, has so far been ascribed to three African species–*Epomophorus gambianus*, *Eidolon helvum*, and *Hypsignathus monstrosus* (Rousselot, 1950; Parker, personal communication, 1976; Charles-Dominique, personal communication, 1977). The first observation, of unidentified species, was made by Prof. J. A. Wahlberg in 1841 near Port Natal, South Africa. The first part of his account reads (in translation): "Port Natal, October 5th, 1841 . . . . Some time ago I shot two species of *Pteropus*, one of which I think may be new (possibly a new genus); it has four upper and five lower cheek teeth." Thereafter he relates how he shot them: in the evening over a spring where they came to drink while flying low over the water (*in* Petermann, 1858). Unfortunately he does not mention the name of the species he knew, which would have given a clue to the identity of the other, supposedly new species. Of the fruit bat species now known to occur there, only *Eidolon helvum* and *Rousettus aegyptiacus* had been described at the time of Wahlberg's writing. Kock's assumption (1969) that an *Epomophorus* species was involved here is probably based on the fact that the holotype of *Epomophorus wahlbergi* (Sundevall, 1846) had been collected by Wahlberg near Port Natal. However, this happened 2 years after Wahlberg's observation and shooting of skimming bats, namely on 27 November 1843 (Andersen, 1912). Moreover, it is clear from Wahlberg's report that his observation applied to both "species" shot by him, one of which he knew (thus probably *Eidolon* or *Rousettus*), and one of which was new to him and which had four upper cheek teeth instead of three as in *Epomophorus*. To my knowledge, cases of additional upper cheek teeth have not been described for this genus (compare the footnote in Andersen, 1912:516). I think, therefore, that Wahlberg had before him a subadult specimen of *Eidolon helvum* or of *Rousettus aegyptiacus* with unerupted M^2 and M_3. Wahlberg's bat collection, now in the Naturhistoriska Riksmuseet in Stockholm, did not contain other Megachiroptera than the just mentioned holotype of *Epomophorus wahlbergi* (Dr. C. Edelstam, letters of 1 April 1976 and 12 September 1977), although it is not impossible that part of his material was lost, as were many of his original notes (Petermann, 1858).

Precise accounts of what African Megachiroptera actually do when skimming over water are very few. In three cases, they are reported to drink somehow directly (Wahlberg, *in* Petermann, 1858; Parker, this paper; Bradbury, this paper). On two occasions, they were seen to dip with some ventral part of their bodies and definitely not with their snouts (Rousselot, 1950; Robelus, this paper), while one of these observers reported that they lick water from their fur afterward (Rousselot, 1950). On yet another occasion three observers saw *Eidolon helvum* dipping with its legs (this paper).

Wahlberg went to the spring where he saw the skimming bats to shoot them in the first place. Moreover he had fires lit at the sides of the spring to enable him to shoot bats coming near the fire, because otherwise he could not hit them. When looking past these fires at the skimming bats, his chances to observe accurately can hardly have been great, to say the least. I know that Parker made his observations without binoculars, while the bats were skimming the water of a scarcely illuminated swimming pool, and he himself was seated at some distance on a well-illuminated terrace. Again, the circumstances were rather poor. Rousselot's paragraph (1950) dealing with skimming *Eidolon* at Ségou is worth quoting (in translation): ". . . they fly very low over the water and only wet the fur of their breast and belly. Having risen immediately thereafter for two or three meters, they lick this wet fur, simultaneously interrupting their flying movements. Then they rise to make up for the lost height and lick again. This happens three or four times, after which they repeat the whole maneuver, until they are satisfied." He wrote that *Epomophorus gambianus* acted in the same way, but where he observed this is not stated. With regard to *Eidolon*, it looks very much like Rousselot may have seen what my companions and I saw at Lake Pandam in Nigeria, in which case the aberrant details in his story could be due to careless observation and interpretation. We observed a flying height of at most 30 to 50 cm. Most of the bats we followed dipped (their legs) only one time, some up to four or five times, and they touched the water each time they were near it (we actually saw the splashes). Their movements down to the water were active and deliberate. We observed no interruptions of wing movements, but of course, the bats had to brake their flight in order to descend. We did not see individuals flying more than one stretch at the reported height.

All in all, the evidence that certain wild African Megachiroptera skim over open water surfaces in order to drink is meager and, in part, doubtful. Of course, it is easily conceivable that at least some species do drink water under certain conditions. Forest species might lap water from small reservoirs of different types, such as holes in trees, but populations inhabiting the dryer savanna regions may have to search for larger bodies of water, such as lakes and streams. This may be true for *Eidolon helvum* in particular, because this species roosts exposed to the sun, unlike other African Megachiroptera, and may need extra water to make up for its potentially stronger transpiration. However, why should they drink by means of the seemingly hazardous skimming maneuvers instead of getting at the water through climbing down to it along tree branches? This latter behavior has been reported for wild specimens of an unidentified *Pteropus* species from Sumatra (van Balen, 1914). Ratcliffe (1961) saw flying foxes (most probably species of *Pteropus*) drinking by the skim-and-scoop method in New South Wales on the Nambucca River in 1930, and offshore on Bougainville, Solomon Islands, in 1945. He tried to explain this by assuming that these bats were drinking salt (or salty) water for the sake of mineral salts, which their normal food would not supply in adequate quantities. His observations on the Bougainville bats reminded me of our own of *Eidolon* at Lake Pandam. He also emphasized the importance of focusing on individual bats to obtain an idea of what they were doing. He observed large groups of bats flying to the sea just after sunset. Each bat would cruise up and down for a while, and then fly right down to the sea once or twice (some three times) and then leave the flying mob and head inland, presumably to set out on its nightly food search. If the water was calm enough, he and his co-observer did see the actual lap-splashes. From the latter remark in his account, it is clear that it must have been very difficult to see (after sunset) whether the bats were scooping water or wetting their fur or dipping their legs. Another interesting report is that of Mr. J. V. de Bruijn (*in* Ripley, 1960), who at the north coast of New Guinea observed large flying foxes trying to pick up fruits, which were floating on the sea surface just offshore. Ratcliffe (1961) thought that these bats may also have been drinking salt water instead of picking up fruits. I do not know of other reports on Megachiroptera outside Africa skimming over water in order to drink. There must be more, because in a popular account on Indonesian flying foxes van Bemmel (1974) wrote (in translation): "Their habit of scooping water while flying low over its surface is well-known." The salt-water story does not hold for the fresh-water skimming African bats, and in general I doubt whether Ratcliffe's conclusion is correct. Many fruit bats will never have an opportunity to drink sea water, and quite a few, apparently, skim over fresh water. Moreover, the wild Sumatran *Pteropus* mentioned by van Balen (1914) drank fresh water, albeit from a hanging posture, and captive *Pteropus giganteus* (Brünnich, 1782) are reported to "drink often, especially during the summer" (Sányál, 1892).

The question remains why *Eidolon*, at least on one well-documented occasion, dipped its legs. One can think of several explanations, none of which seems good enough. *Rousettus aegyptiacus* in the Amsterdam zoo not only drinks from its water bowl, but also uses it to take baths. A freshly bathed bat licks itself and is licked by the others (Mr. F. Gangel, personal communication, August 1977). This could hardly be a way of drinking, as the animals also drink "normally." Could it be a means to clean the body, maybe even of certain parasites, or could it have some thermoregulatory function? If one of these questions would eventually produce a satisfying explanation with regard to *Rousettus*, would this explanation also satisfy us with regard to the wild, leg-dipping *Eidolon*? I do not think so. In this regard, *Eidolon helvum* is easy to study, as it roosts in large numbers and fully exposed near many human settlements. It is known that *Eidolon* passes its day, like so many other mammals, partly with grooming its body and fur. It is also sufficiently known that common external parasites of *Eidolon*, such as the nycteribiid fly, *Cyclopodia greeffi* Karsch, and the spintumicid mite, *Meristaspis* sp. (Adeosun, 1974), have no preference whatsoever for the legs or lower abdomen of their hosts. Moreover these parasites attach themselves so firmly to the skin of the bat that a little water will not harm them in the least. Likewise, a thermoregulatory purpose of the wetting of so small a part of the body is hard to understand.

Another possibility is that the water itself does not play the important role, which we have tried to attach to it. Could *Eidolon* be picking something out of the water (as there were, on Lake Pandam, hardly any fruits, these can be disregarded)? Could *Eidolon* possibly be fishing? Carnivorous behavior has recently been reported of two other African Megachiroptera. Van Deusen (1968) cited someone, who observed wild *Hypsignathus monstrosus* pick up and eat the skinned bodies of birds, which had been tossed outside a house, and also how it attacked live chickens near the same house, at M'Bigou in Gabon. Coe (1976) kept *Lissonycteris angolensis* (Bocage, 1898) in a cage together with *Myonycteris torquata* (Dobson, 1878), at Mount Nimba, Liberia, and saw how specimens of the former species actually attacked and devoured specimens of the latter. It is of interest to quote here (in translation) the report on a Sumatran *Pteropus* by van Balen to which I referred before in relation to its drinking behavior. "My son Mr. D. J. van Balen, living at Serbadjadi (Galang), Deli, observed that kalongs (=flying foxes) do drink. He used to spend the night now and then on a platform in a forest tree to watch animals. One night he saw a number of flying foxes alight in a dead tree, climb down along branches which hang over the water of a deep pool, and drink while hanging from these branches. After drinking they let themselves fall onto the surface of the water, where they stayed for some moments, constantly flapping their wings, and then flew up in the limited space in circular movements until they could take flight in the open air above the trees." This observation was repeated on request, and I think it should be taken seriously. Later, van Balen's son was told by a native that the flying foxes did not descend to the pool to drink, but to catch the little fishes which abounded in such pools. Dr. F. A. Jentink, the well-known Dutch mammalogist, wrote to van Balen that he did not believe that kalongs drank, and he warned him against native stories. But why then, asked van Balen, would kalongs perform such breakneck stunts? (van Balen, 1914).

Apparently this belief in fishing kalongs is more widespread (though not so much in the literature), as van Bemmel (1974) also mentioned it (and rejected it). Apart from the hint at possible piscivorous behavior of *Pteropus* van Balen's account (1914) deals with another aspect of the relation between Megachiroptera and water. It confirms that they, or at least certain *Pteropus* species, can swim. Ryberg (1947) cited Trouessart's story on how, during James Cook's second journey around the world (1772–1775), swimming Megachiroptera were observed in the Tonga Archipelago. These were probably *Pteropus tonganus* Quoy & Gaimard, 1830. Some of the fruit bats seen picking up fruits from the sea surface in North New Guinea (Ripley, 1960) "dipped too far into the water, became caught and splashed in. The instant this happened, the flying foxes came to rest quietly on the surface with wings well spread. Thence they gradually rode in on the waves of the rising tide. The sea was not too rough, and gradually they tumbled into the light surf and quickly proceeded to drag themselves out of the wave area. Without exception, the bats then crawled up the beaches, occasionally shaking themselves, and made for the low dunes above high water mark." Beyond these dunes the bats climbed up small trees and launched themselves into the air again. Novick and Leen (1969) gave a splendid series of photographs of a swimming *Pteropus giganteus* (Brünnich), but unfortunately it is not stated where they were taken. Van Bemmel (1974) knew of a *Pteropus* kept as a pet on a houseboat on Sumatra. This animal once fell into the water. Thereafter, it made a daily habit of plunging into the water and swimming about for a while (until, 2 years later, it was seized by a crocodile).

Summarizing, it has not yet been sufficiently documented that, in the wild, African Megachiroptera need to drink water. In captivity *Rousettus aegyptiacus* and *Eidolon helvum* may drink from bowls, and *Hypsignathus monstrosus* is reported to drink through the skim-and-scoop method. In the wild *Eidolon helvum* and *Epomophorus gambianus* have been seen to skim over open water, but none of the reports in which they would do so in order to drink seem to stem from really careful observation. The behavior of captive *Hypsignathus monstrosus* and of many wild Microchiroptera supports the idea that physically Megachiroptera may be able to drink while skimming. *Eidolon helvum* has been seen to skim over open water not to drink but to dip its legs for an unknown purpose. Of skimming and swimming Australasian species of the genus *Pteropus* (which in its ecology and ethology shows a great resemblance to *Eidolon*) it has been suggested that they might be fishing, and as carnivorous behavior has been reported for some African fruit bats, I do not exclude fishing as a possible explanation for the leg-dipping of *Eidolon*. Against this would be that *Eidolon* is also attracted by swimming pools, but I do not suggest that drinking as one of the possible aims of skimming Megachiroptera should be neglected. More critical observation in the wild, and possibly some experimenting with captive fruit bats (large enclosures with large, fish-inhabited water containers on the floor; small, whole fishes as part of their diet) should provide the final answers.

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ECOLOGICAL POSITION OF THE FAMILY LORISIDAE COMPARED TO OTHER MAMMALIAN FAMILIES

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ABSTRACT

African primates of the family Lorisidae are compared to other families of African mammals from the perspective of ecological niche occupancy. It is shown that lorisids, along with other rodents and carnivores, occupy an ecological niche characterized by arboreal-nocturnal-climbers and/or leapers-animalivores-frugivores-gumivores habits (A.N.C.L.A.F.G.). Generally, mammals (especially primates and carnivores) occupying this type of niche exhibit many primitive evolutionary characters.

INTRODUCTION

Among primates, Strepsirhini (Afro-Asian and Madagascan lemurs) represent 18% of the living species. In terms of their anatomy, physiology, and behavior, they are considered more primitive than the "higher primates" (Catarhini and Platirrhinii). Although five Malagasy families (of which two are subfossils) are the result of a radiative evolution, the Cheirogaleidae and the Lorisidae (in Africa and South Asia) have retained numerous primitive features (Charles-Dominique and Martin, 1970). The taxonomic position of these two groups have been discussed by different authors (Cartmill, 1975; Charles-Dominique and Martin, 1970; Charles-Dominique, 1977; Goodman, 1975; Hoffstetter, 1974, 1977; Martin, 1972; Pocock, 1918; Simpson, 1945; Szalay and Katz, 1973; Szalay, 1975; Tattersall and Schwartz, 1975; Van Kampen, 1905; Van Valen, 1969; Weber, 1928). According to the interpretation of early primate history by each author, the Lorisidae and Cheirogaleidae have been classified either in two different suborders, two different families, or two different subfamilies. Nevertheless, even if the Cheirogaleidae and the Lorisidae have been geographically separated since the early Tertiary, they share numerous characters inherited from a common ancestor, and presently occupy similar ecological niches.

In this paper, the ecological position of one of these two primitive families (Lorisidae) and its relationship to other mammalian groups living in the same forest ecosystem are discussed. Different ecological parameters shall be analyzed including diet, activity rhythms (nocturnality or diurnality), habitat preference, and locomotor patterns.

FOOD PROVIDING ENERGY AND FOOD CONCERNED WITH THE RESTORATION OF TISSUES

It is necessary to make a distinction between food which is used for energy (glucids) and food which balances the loss due to tissue turnover (for example, loss of proteins, see Hladik, 1977).

Food providing energy.—Every molecule catabolized by an organism can be used for energy. For example, strict carnivores and strict insectivores (="animalivores") use glucids, lipids, and proteins for energy. Proteins are difficult to find in large quantities and many animals eat small quantities of proteins necessary for their balance, but use lipids and especially glucids as energetic food. Soluble glucids (C5, C6, and C12 sugars) are directly assimilable by a nonspecialized gut. They are found in fruits like berries, drupes, and so on (especially in fruits with a fleshy pericap around the stone). Nonsoluble glucids (celluloses, hemicelluloses, and others) are made up of soluble sugars polymerized in complex chains. Mammalian enzymes cannot break these long chains, but they are hydrolized by bacteria in specialized digestive ducts (stomach of ruminants, saculated stomach, caecum). Celluloses and hemicelluloses are the principal constituents of leaves and wood. Gums are produced by some trees and lianas after different actions (insect bites, xylophages, other injuries). Composed of C5 and C6 sugars polymerized in long chains, they are biodegraded in the caecum by bacteria (for Prosimians).

Food concerned with the restoration of tissue.—In addition to vitamins and mineral elements, which are generally present in sufficient quantities in natural food, amino acids (associated in proteins) play a major role in the constitution of the tissues (turnover, growth, gestation, and lactation). In the forest, proteins can be found in prey, in kernels, and in the green part of plants (especially young shoots). These three sources are correlated with different specializations: prey capture is correlated with morphological and behavioral specializations of predators; kernel and seed intake is correlated with dental specializations allowing opening of hard stones, and gut specializations for detoxification of secondary compounds often present in seeds; leaf intake is correlated with the specialization of the digestive duct. This last solution, generally used by animals which can digest the cellulose, requires large quantities of bulky food relatively poor in assimilable proteins.

As "energetic food," proteins can be a limiting factor for animal populations.

NOCTURNALITY AND DIURNALITY

Theoretically, food resources are available around the clock but consumers are generally specialized to feed during either the day or night (Charles-Dominique, 1975). It seems that among higher vertebrates, birds are specialized to the diurnal way of life and mammals to the nocturnal. Of course, secondary specializations allow some birds to feed during the night and some mammals to feed during the day, but they are limited. For example, in the Gabon forest, 70% of the mammals are nocturnal, 10% are nocturnal and diurnal, and 20% are strictly diurnal (among 120 species of mammals); in the same ecosystem, 96% of the 216 bird species are diurnal. The same picture exists in the tropical forest of Panama where 86% of the mammals are nocturnal, 6% nocturnal and diurnal, and 8% strictly diurnal (Eisenberg and Thorington, 1973). The diurnal mammals compete successfully in four different ways, which can be listed as follows: increase in body size (monkeys, apes, antelopes, and big carnivores); continually growing incisors (a system which enables squirrels to open tough fruits and nuts); claws to dig out hidden prey (some squirrels, Callitrichidae monkeys, and some anteaters); development of intelligence (especially for monkeys).

In terms of competition for food, it is necessary to separate the "nocturnal world" from the "diurnal world."

ECOLOGICAL POSITION OF THE FAMILY LORISIDAE

Lorisids (10 species of which there are eight in Africa) are all arboreal, nocturnal animals. They find proteins by hunting prey; the energetic food is found mainly in soluble sugars (soft fruits) and/or in gums which are biodegraded in the caecum. Secondary specializations allow several species to live sympatrically, avoiding competition for food. For example, five species of Lorisidae live in the same ecosystem of the rain forest in Gabon (two lorisinaes = slow-moving climber animals and three galaginaes = fast-running and leaping animals). The two Lorisinae (*Arctocebus calabarensis* and *Perodicticus potto*) are specialized in the capture of irritant and pungent-smelling prey ignored by the three Galaginae species (*Galago elegantulus*, *G. alleni*, and *G. demidovii*). *A. calabarensis* live in the understory, in recent tree-fall zones and *P. potto* in the canopy. An equivalent separation exists among the three galaginaes—*G. elegantulus* live in the canopy where they feed on insects and gums; *G. alleni* live in the undergrowth and feed on insects and fruits; *G. demidovii*, the dwarf bushbaby, hunt prey (70% of their diet) in thick vegetation composed of a mixture of lianas and tree foliage (Charles-Dominique, 1971, 1977). *A. calabarensis* and *G. demidovii* are the two smallest species of their respective subfamilies. They succeed in feeding almost entirely on prey (85% and 70%). The three other much larger species capture the same absolute quantities of prey but they must complement this food by fruits and/or gums (food providing energy).

The ecological niches of the Lorisidae can be defined as Arboreal-Nocturnal-Climbers and/or Leapers-Animalivores-Frugivores-Gumivores (=A.N.C.L.A.F.G.).

DIRECT COMPETITORS OF THE LORISIDAE

The Lorisidae are not the only mammals to occupy such ecological niches (A.N.C.L.A.F.G.); in Gabon, the Paradoxurinae *Nandinia binotata* (palm civet) and several rodents can be found in them: *Graphiurus murinus* (Gliridae), and *Thamnomys rutilans, Praomys tulbergi, Praomys lukolelae, Stochomys longicaudatus, Hylomyscus stella, Hylomyscus fumosus, Hylomyscus aeta,* and *Hylomyscus parvus* (Muridae).

With the exception of *Graphiurus murinus* and *Thamnomys rutilans*, which are true arboreal animals, these species generally live at a lower level of the forest but can interfere with lorisids in the undergrowth. Because of a poor knowledge of their ecology, an estimate of the total number of A.N.C.L.A.F.G. mammals is between eight and 15 species. In addition, other categories of sympatric mammals whose diet can interfere with those of A.N.C.L.A.F.G. mammals must be considered (for example, some bats which hunt prey hidden in the foliage).

The more complex the forest, the more different biotopes and, thus, different ecological niches it presents. In Gabon, where the forest is one of the most complex in the world (1,000 to 2,000 species of trees and lianas) eight to 15 mammal species occupy these A.N.C.L.A.F.G. ecological niches (among 120 sympatric mammalian species). In comparison, the dry forest of the west coast of Madagascar (Morondava region) is composed of about 150 species of trees and lianas; only five species of mammals (four primates—*Microcebus murinus, Microcebus coquereli, Cheirogaleus medius,* and *Phaner furcifer*—one rodent—*Eliurus* sp.) occupy the A.N.C.L.A.F.G. ecological niches among 19 sympatric mammalian species. In South Africa and East Africa, gallery forest and woodland-savanas are poor in species of trees and lianas (about 100 species per ecosystem); only one species of Lorisidae, or rarely two (*Galago senegalensis* and/or *Galago crassicaudatus*), can be found in these ecosystems (Bearder, 1974; Bearder and Doyle, 1974).

Population densities change as a function of the abundance of arboreal mammalian species in relation to the complexity of the forest. In Gabon, if we consider the five lorisid species together, they form an overall population of about 160 individuals/square km. In South Africa and East Africa, the population of *Galago senegalensis* and/or *Galago crassicaudatus* is generally more abundant—110, 112, 125, 175, 183, 200, 175, 500 individuals/square km according to the area (Bearder, 1974). In the dry forest of western Madagascar, the four primate species, ecologically equivalent to the Lorisidae (Cheirogaleidae) form an overall population of about 500 individuals/square km (Charles-Dominique and Petter, 1978).

At first sight, in spite of the scarcity of plant and animal species, the animal populations of dry forests are highly concentrated (Table 1). In fact, for an ecosystem we must consider all the species occupying the A.N.C.L.A.F.G. ecological niches. In Gabon, the Lorisidae constitute only five of the eight to 15 mammalian species adapted to these niches; the bushbabies in South Africa and the Cheirogaleidae in western Madagascar are practically the only species to occupy homologous ecological niches in their respective ecosystems. At the present time, it is impossible to make an evaluation in Gabon, but it is probable that the overall density of the eight to 15 Gabonese species living in A.N.C.L.A.F.G. niches (or at least their biomass) is roughly equivalent to those calculated for their relatives in dry forests.

In the Gabon rain forest ecosystem, the different families which occupy similar niches of the A.N.C.L.A.F.G. categories avoid food competition by developing some morphological, ethological, and physiological specializations, in the same manner as the different lorisid species avoid food competition. These specializations are differences in body weight (rodents—10 to 50 g; lorisids—60 to 1,000 g; palm civet—2,000 to 4,000 g, and prey capture techniques (prey size is generally related to predator size).

Bushbabies detect prey by vision and hearing. Capture is achieved by a rapid stereotyped movement of the hand, often when the insect is flying or ready to escape (Charles-Dominique, 1971, 1977). This elaborate system provides the bushbabies with exclusive access to some categories of mobile prey living in the foliage.

CONCLUSION—DISCUSSION

If animals which are phyletically as different as the primates, rodents, and carnivores discussed in this paper can occupy ecological niches of the A.N.C.L.A.F.G. types (Arboreal, Nocturnal,

Table 1.—*Comparative situations of A.N.C.L.A.F.G. (=Arboreal, Nocturnal, Climber/Leaper, Animalivore-Frugivore-Gumivore) lemurs (Lorisidae in Africa. Cheirogaleidae in Madagascar) and sympatric mammals in three different ecosystems*—Gabon, *rain forest of Makokou area;* South Africa, *different gallery forest and wooden savannas of Transvaal, Zululand, and eastern Rhodesia;* Madagascar, *West Coast, Morondava area. Even with a higher number of species, the lemurs of the rain forest occur in lower population densities compared to dry forest species. This low value, in rain forests, can be related to the presence of numerous other mammalian competitors living in sympatry (A.N.C.L.A.F.G. mammals).*

Parameters	Gabon rain forest	South Africa dry forest	Madagascar dry forest
Number of plant species (trees—shrubs—lianas)	1,000–2,000	#100	#150
Number of sympatric mammals	120	?	20
Number of sympatric arboreal mammals	38	10–15	8
Number of sympatric A.N.C.L.A.F.G. mammals	8–15	#5	#5
Number of sympatric A.N.C.L.A.F.G. lemurs	5	1–2	4
Total density of sympatric A.N.C.L.A.F.G.* lemurs (square km)	160	110–500	600

Climber/Leaper, Animalivore-Frugivore-Gumivore), it is probably because these modes of life do not require such complex specializations as animals exploiting areas or food of "difficult" access. In South America, the didelphid marsupials of the genera *Marmosa, Philander,* and *Caluromys,* which present numerous primitive characters, also occupy similar ecological niches. The Jurassic panthotherian (140 million years old) found in Portugal is considered to have been insectivorous and arboreal in habits (Buffetant, 1977) probably close to those observed for the above species.

One can consider that these modes of life were adopted very early by different primitive mammals which, later, could give rise (or not) to taxa ecologically adapted to other types of life.

Among strepsirhines (African and Malagasy lemurs) the two families presenting the greatest number of primitive characters—Lorisidae and Cheirogaleidae—occupy ecological niches of the A.N.C.L.A.F.G. type. The situation is identical to that of Paradoxurinae (palm civets) as compared to other subfamilies of Viverridae. These A.N.C.L.A.F.G. ecological niches can be considered as "conservative"; they are not related to major modifications of the primitive mammalian model. Among Muridae, most of which are terrestrial or semiterrestrial animals, some species have been able to colonize these ecological niches without developing particular adaptations.

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THE IDENTITY OF *GERBILLUS BOTTAI* LATASTE, 1882 (MAMMALIA: RODENTIA), FROM SENNAR, SUDAN

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ABSTRACT

Two recently collected gerbils from the Gezira, Sudan, are identified as *Gerbillus bottai* Lataste 1882. They are compared with other species of the subgenus *Hendecapleura* (*campestris*, *c. wassifi*, *nanus*, *n. garamantis*, *pusillus*, *harwoodi*, *watersi*, and *henleyi jordani*) and discussed with further described taxa (*stigmonyx*, *luteolus*, *venustus*). The proposal is made to consider *G. stigmonyx* as a *nomen dubium*, and to unite *G. luteolus* and *G. harwoodi* under the older name *G. bottai*.

The use of the geographical name Sennar is briefly explained for a more careful consideration in connection with restrictions of type localities and animal distribution.

INTRODUCTION

During an investigation of harmful rodents in the Sennar region of the Sudan, Mr. Arno H. Hoppe of the Deutsche Gesellschaft Für Technische Zusammenarbeit (GTZ) collected several specimens of small mammals, which were sent for identification to the Forschungsinstitut Senckenberg, Frankfurt a.M. Among the specimens received were *Crocidura s. sericea* (Sundevall 1843) from Fadasi Halimab (Southern Gezira Dist.), *Crocidura flavescens hedenborgiana* (Sundevall 1843) from Ma'tuq (Dueim Dist.), *Arvicanthis abyssinicus* (Ruppell 1942) from Fadasi Halimab and Wad Medani, *Mastomys natalensis macrolepis* (Sundevall 1943) from Wad Medani and Barakat (Southern Gezira Dist.), *Taterillus gyas* Thomas 1918 and *Acomys dimidiatus* (Cretzschmar 1826) from Gadambalia (Gedaref Dist.), and two gerbils discussed below.

SYSTEMATIC DISCUSSION

Gerbillus (Hendecapleura) bottai Lataste, 1882

Specimens examined.—Bageir = El Baqeir, Northern Gezira Dist., Blue Nile Prov., 15°21′N, 32°45′E, 1♀ (skin, skull) SMF 50158; Managil, Southern Gezira Dist., Blue Nile Prov., 14°15′N, 32°58′E, 1♀ (skin, skull) SMF 50159.

Comparative material of the subgenus Hendecapleura *Lataste 1882.*—*G. campestris* LeVaillant, 1857: S. W. Matmata, S. Tunisia, 2♀ (2 skins, 2 skulls) SMF 52328, 52329; El Goléa, Algeria, 1 sex unknown (skin, skull) SMF 51629; Imlaoulaouen, Hoggar, Algeria, 1♂ (skin, skull) SMF 51630; Guelta Afilale, Hoggar, Algeria, 1♂, 4 sex unknown (5 skins, 5 skulls) SMF 51631–51635. *G. campestris wassifi* Setzer, 1958: Bahig, Western Desert, Egypt, 2♂, 1♀ (3 skins, 3 skulls) SMF 26804–26806. *G. n. nanus* Blanford, 1875, Rafsanjan, Kerman Prov., Iran, 1♀, 3♂ (4 skins, 4 skulls) SMF 46370–46372, 46374. *G. n. garamantis* Lataste, 1881: Oued Noun, S. E. Goulimine, S. Morocco, 7♂, 2♀ (7 skins, 2 alc., 9 skulls) SMF 47676–47684. *G. stigmonyx* Heuglin, 1887: Jebelein, E. bank White Nile, Blue Nile Prov., Sudan, 1♀ (skin, skull broken) AMNH 82219. *G. pusillus* Peters, 1878: Iraka, Tanzania, 2♀ juvenile (2 alc., 1 skull) SMF 11494, 11495. *G. harwoodi* Thomas, 1901: Mt. Suswa, Rift Valley, Kenya, 10 sex unknown (broken skulls from owl pellets) SMF 41513–41519, 41527, 41530–41531; S. shore L. Naivasha, Kenya, 1♀ juvenile (alc., skull) SMF 42297 [This species averages larger (most obvious in M^1-M^3) than the sympatric *G. pusillus* (Petter, 1975; Roche 1976)]. *G. watersi* DeWinton, 1901: Shendi, Northern Prov., Sudan, 2♂ (2 skins, 2 skulls) B.M. 1.5.5.55, 1.5.5.56 (paratypes). [Listed by Petter (1975) as a valid species and as a subspecies of *G. nanus*, said to occur in Upper Nile, Sudan, which places it in the southern Sudan. The occurrence of a subspecies of *nanus* in the horn of Africa besides *watersi* (Petter, 1975; Roche, 1976) hints to the specific validity of *watersi*.] *G. henleyi jordani* Thomas, 1918: Gabès, Tunisia, 1♂, 1♀ (2 skins, 2 skulls) SMF 19543, 19544; Jebel Mrhila, Tunisia, 2♀ (2 alc., 1 skull) SMF 28598, 29599.

Lataste (1882*a*) recognized the new species *G. bottai* (two skulls, one skin from Sennar, collected by Botta in 1834) among misidentified gerbils and had already used the new name in a session of the Societé Zoologique de France on 13 December 1881 in explaining the synonymy of *Gerbillus gerbillus* Olivier, 1801 (Lataste, 1882*b*), but the original description was not published until 1 March 1882 (Lataste, 1882*c*).

This description is based on two skulls and one skin with incomplete tail; the latter nearly unicolored, dorsal coloration not clearly set off from ventral side; hind feet naked, shorter than in *G. quadrimaculatus* Lataste, 1882, from Nubia, a supposed synonym of *G. campestris* LeVaillant, 1857. The two skulls were both 25 mm long (which is probably

Table 1.—*External and cranial measurements of selected specimens of the genus* Gerbillus.

Measurements	Holotype *G. bottai* Lataste, 1882*c*	B.M.21.-4.18.6 juv. Sennar		SMF 50158 ♀ El Bageir	SMF 50159 ♀ Managil	Holotype *G. luteolus* ♂	AMNH 82219 *G. stigmonyx* ♀	*G. stigmonyx*, Setzer, 1956		Holotype *G. harwoodi* ♀ Thomas, 1901	SMF 41513-9, 27, 30, 31 Rift Valley
		Setzer, 1956	Present study					♂	♀		
Head and body length	85	—	—	86	85	95	90	87	—	82	—
Tail length	[62]	—	—	107	93	110	93	104	—	113	—
Hind foot length	20	—	—	21	22	23	21	20	—	22	—
Ear length	6	—	—	11	11	12	—	—	—	10	—
Greatest length of skull	25	22.7	22.6	26.5	26.3	28	—	27.3	26.5	26	—
Condylobasal length	—	19.6	20.6	24.0	24.3	—	—	24.8	23.6	—	—
Basilar length	—	—	—	22.0	21.9	21	—	—	—	19	—
Mastoid breadth	—	—	—	11.7	11.3	—	—	—	—	—	—
Braincase breadth	—	—	11.0	12.1	11.8	12.2	—	13.5	13.6	12	—
Zygomatic breadth	—	—	—	14.1	13.7	14.0	—	14.2	14.2	—	—
Interorbital breadth	—	4.2	4.0	4.8	4.5	4.8	4.4	4.9	4.9	4.5	4.3–4.8; M = 4.5; N = 7
M^1-M^1 breadth, crown	—	—	4.9	5.4	4.9	—	5.5	—	—	—	5.0–5.2; M = 5.1; N = 3
M^1-M^1 breadth, alveolar	—	—	4.2	4.9	4.7	—	4.7	—	—	—	4.7–4.9; M = 4.8; N = 4
Diastema length	—	—	5.2	6.7	6.8	7.2	7.0	—	—	6.5	5.8–6.4; M = 6.2; N = 9
For. incisiv. length	—	3.8	4.0	4.3	4.3	4.7	4.5	4.9	4.7	5	4.3–4.8; M = 4.7; N = 9
Nasal length	—	7.8	7.4	9.7	8.6	10	9.9	9.9	9.8	10	—
Bullae length	—	7.4	6.2	9.4	9.7	—	9.6	9.4	9.4	—	—
Mandible angular	—	—	—	12.9	12.8	—	12.8	—	—	—	—
Mandible condylar	—	—	—	13.7	13.8	—	13.6	—	—	—	—
M^1-M^3 crown	—	3.8	3.5	3.6	3.5	3.6	3.5	3.7	3.8	3.6	3.40–3.83; M = 3.60; N = 9
M^1-M^3 alveolar	—		—	4.1	3.7	—	4.2	—	—	—	3.75–4.20; M = 3.92; N = 9
M_1-M_3 crown	—	—	—	3.5	3.4	—	—	—	—	—	—
M_1-M_3 alveolar	—	—	—	3.6	3.6	—	—	—	—	—	—
M^1 breadth	—	—	1.3	1.3	1.3	—	1.25	—	—	—	1.20–1.38; M = 1.30; N = 10

the total occipital-nasal length) and nearly as large as in *G. quadrimaculatus*, that is, somewhat shorter; posterior border of interparietal bone salient in the middle, which instead of being concave, is a transversal rhomboid with rounded corners; incisors less strongly colored, the molars heavier than in *G. quadrimaculatus*.

G. bottai differed from *G. garamantis* by narrower posterior region of the skull, less inflated bullae, and lighter molars. In *G. garamantis*, the interparietal bone is concave, foramen incisivum remains well away from the molars, and the palatine foramina start from the first tubercle, not from the following lamina of M^1 as in *G. bottai*. The remaining comparisons were made with forms of the subgenus *Gerbillus*.

In the course of a series of papers, Lataste included *bottai* in the new subgenus *Endecapleura* Lataste, 1882*d* (later emended to *Hendecapleura* by himself) with a question mark only, together with *garamantis* Lataste, 1881 (genotype), *nanus* Blanford and possibly *Quadrimacutatus* (sic) Lataste, 1882.

The two new specimens now under discussion agree well in size with the original description of *bottai* (Table 1), but not in the form of the interparietal bone, the situation of the incisive and palatine foramina, and separation of coloration between dorsal and ventral side.

However, *G. garamantis* from southern Morocco also does not fit the comparison given by Lataste (1882*c*). Because of the missing tail tip in the only skin of *G. bottai*, nothing is known about the form of the tuft.

The two new specimens have tails longer than the head and body (Table 1), slightly darker above, with a weakly developed tail tuft, dorsal and ventral color clearly separated; clear white postorbital and auricular spots; hind foot relatively broad, middle finger not elongated and approximately one-fourth of the total hind foot length; and a few short hairs scattered on the distal part of the hind foot.

Nothing was said of the deposition of the original material; Thomas (1919) noted that the specimens were not in the Lataste collection received at the British Museum, but confirmed DeWinton (1901) that *G. bottai* was based on specimens in the Paris Museum. However, Rode (1945) did not list *G. bottai* among the type specimens of Gerbillinae.

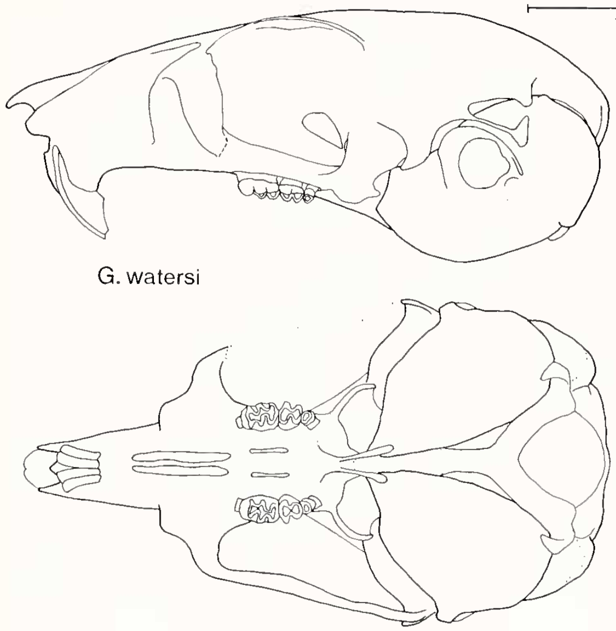
There are apparently only two specimens of *G. bottai* available for study in the British Museum; these were examined by Setzer (1956). One of them was collected by S. S. Flower (B.M. 21.4.18.6, skin and skull of a juvenile) at Sennar, Blue Nile, and the older one (B.M. 46.6.2.44, skin in poor condition), by Hendenborg in Sennar, was received in exchange from the Stockholm Museum by Sundevall. Without a doubt, these specimens, one younger and the other older than the original description, could have been identified only by comparison with the description.

One of the recent specimens (SMF 50158) was sent to the British Museum for direct comparison with the two unique *G. bottai* (Table 1). The results (including the above details of the British Museum specimens of *G. bottai*) were thus (I. R. Bishop in litt., 20 April 1977; P. D. Jenkins in litt., 20 August 1977): "Apart from the difference in size, the young skull differs from your specimen in that the lateral pterygoid fossae are smaller and hemispherical in shape. The supraorbital ridges not so pronounced and the lip of the auditory meatus less prominent." These discrepancies can all be attributed to differences between juvenile and adult skulls.

Furthermore (Jenkins in litt., 25 August 1977) "both B.M. skins have white patches behind the ear but not so distinct as in your specimen. The dorsal coloration is similar although the flanks are not so bright. The ventral is pure white [as in the two recent specimens, author]. The tail of the young specimen is apparently entire and shorter in length than the head and body, unlike your specimen. The tail of our other specimen is broken (B.M. 46.6.2.44) but bears the following comment on its label: 'other specimen sent by Sundevall has tail 115 mm long.' " This 'other' specimen remains unknown. Differences between the recent specimen and the British Museum *bottai* might be attributed to age (changes of which are completely unknown). All subsequent conclusions and measurements, especially of the single juvenile, are necessarily based on that material.

Allen (1939) listed *bottai* as a species of the genus *Dipodillus* Lataste, 1881 which, in his use of this taxon of naked-footed gerbils, included short-tailed as well as long-tailed species of gerbils. Ellerman (1941) regarded *Dipodillus* (including *Hendecapleura*) as one of the two subgenera of *Gerbillus* Desmarest, 1804, but did not allocate *bottai* to either of the two taxa and did not list it under the forms seen, despite two specimens present in the British Museum.

The identification of specimens recorded for the Air region (Niger) as *G. bottai* by Dekeyser (1950)



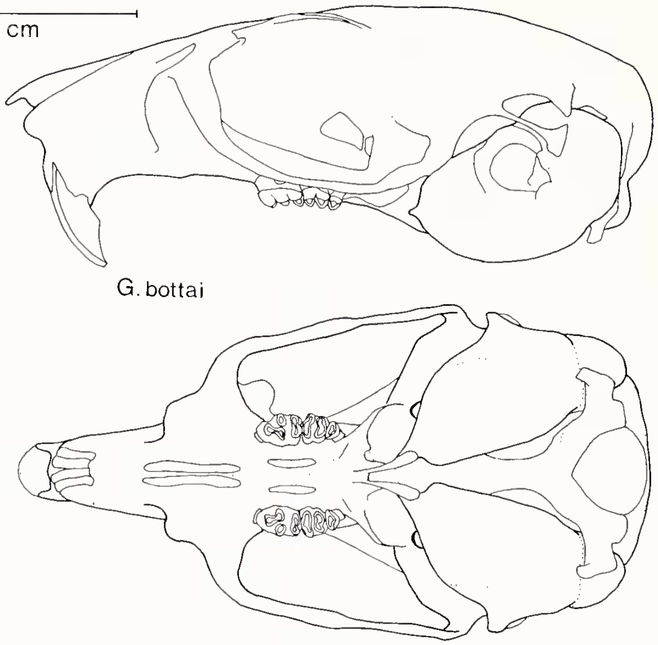


Fig. 1 (left).—Skull of *Gerbillus (Hendecapleura) watersi* (B.M. 1.5.5.56) lateral (upper) and ventral (lower) side. Fig. 2 (right).—Skull of *Gerbillus (Hendecapleura) bottai* (SMF 50159) lateral (upper) and ventral (lower) side (all drawings by Gieela Krebs).

seems highly doubtful and has not been confirmed (compare Petter 1975). The length of the upper molar row is shorter (3.0–3.2) than in *G. bottai* and the specimens were discussed as related to *G. principulus* Thomas and Hinton, 1923 (a subspecies of *G. nanus* with large bullae), and *G. stigmonyx luteolus* Thomas, 1901. Setzer (1956), within the subgenus *Dipodillus*, accorded a separate grouping to *bottai* because of small auditory bullae, open pterygoid fossae (but see note on juvenile B.M. skulls above), and more massive cheekteeth in proportion to the size of the skull, which is confirmed by the present material; *G. bottai* differing mainly in size from *G. stigmonyx* Heuglin, 1877, and *G. lowei* Thomas and Hinton, 1913. A third group, including *G. watersi* DeWinton, 1901, *G. mackillingini* Thomas, 1904, *G. principulus* Thomas and Hinton, 1923, and *G. muriculus* Thomas and Hinton, 1923, is similar to *G. bottai* in body size, but the group differs by more greatly inflated auditory bullae, relatively closed pterygoid fossae, and small cheekteeth. The last three taxa are currently considered to be subspecies of *nanus* and the differences noted by Setzer (1956) are confirmed by the material listed above.

Petter (1968, 1975) states that no external measurements of the only two existing *G. bottai* specimens are known, but in his key this species is differentiated from others by a tail shorter than the head and body length. This confirms the conclusion that *G. bottai* is represented only by the specimens in the British Museum, the skins of which are without measurements (Setzer, 1956) and one of which has a broken tail. The two recent specimens from the Sennar region differ from *G. nanus* by considerably narrower braincase, narrower interorbital width, much smaller bullae, and thus with pterygoid fossae more open, a larger suprameatal triangle, and heavier cheekteeth. They differ from *G. garamantis* and also from *G. watersi* (Fig. 1) by larger skull, heavier cheekteeth, less inflated bullae, and more open pterygoid fossae; *G. watersi*, however, has a thin tuft on the tail (like *G. bottai*).

Both recent specimens differ from *G. pusillus*, of which only a juvenile skull is available to me, by slightly larger molars, second lamina of M^3 reduced to a single cusp, and lighter colored incisors. They differ from *G. henleyi jordani* by larger size in all skull measurements; relative to the size of skull the bullae are less inflated in their anterior part.

G. campestris venustus (Sundevall, 1843), as identified and recorded by Happold (1967*b*) from east of the Nile north of Khartoum and from north of the Blue Nile, is larger in all measurements and has long fur and a heavy tuft on the tail. The *G. cam-*

pestris specimens listed above differ in the same way and additionally have a more closed pterygoid fossae.

The description of *Meriones stigmonyx* Heuglin, 1877, regarded as a subspecies of *G. campestris* (see Petter, 1975), is insufficient for a specific determination, except for its long tail (head and body 71.4–78, tail 104–120, hind foot 19.3, ear 10.8–13.0; converted from "pied du roi" = French foot, 1 line = 2.174 mm). This insufficiency was noted by Thomas (1901) who additionally remarked that a specimen in the Stuttgart Museum, identified as *G. stigmonyx*, does not agree with Heuglin's (1877) description.

Despite these facts, *G. luteolus* Thomas, 1901, was attached to *G. stigmonyx* as a subspecies. The skull measurements of *G. s. luteolus* show only a fair agreement with the two recent specimens, which might be due to different methods of taking measurements. *G. s. luteolus* bears close resemblance to the two specimens under discussion in the distribution of white on the head, including a darker nose patch, and with some tiny scattered hairs in the distal part of the hind feet. This is also the main character by which Thomas (1901) separated *G. s. luteolus* from the more northern (sic) *bottai*. This gerbil has been recorded from the area between the White Nile and Blue Nile (in other words the Gezira) as *G. stigmonyx* (including *luteolus* as a synonym) by Setzer (1956). The type locality of *G. stigmonyx* was given as "near Khartoum" but there is no convincing reason to restrict it to the south side of Khartoum.

As understood by Happold (1967*b*), *G. stigmonyx* has some resemblance with the specimens discussed here; it is smaller than *G. campestris venustus*, with shorter fur and less tufted tail.

An additional specimen of this group from Jebelein (AMNH 88219) agrees well with the characters given above (for measurements see Table 1)—naked and short hind feet, nearly unicolored and weakly tufted tail, postauricular spot not very prominent (like the B.M. specimen), hairs of underside pure white, nose spot not set off from color of head, M^3 with only one lamina (as approached by the left M^3 of SMF 50159), and bullae small.

Happold (1967*a*) does not give locality records for gerbils within the Khartoum Province, but his *G. campestris venustus* were collected north of the Blue Nile (Happold, 1967*b*), only *G. watersi* was recorded from south of Khartoum (Happold, 1969), and no gerbils were found in the Funj area. Thus, *G. stigmonyx*, *bottai*, and *watersi* are the only naked-footed gerbils recorded from the region between the two Niles in the Sudan.

In the combination of characters as detailed above, there are no similar species of either *Dipodillus* or *Hendecapleura* known from Egypt (Flower, 1932; Setzer, 1958; Hoosgtraal, 1963) or Libya (Ranck, 1968).

Of northeastern African *Hendecapleura*, larger size excludes *G. campestris somalicus* Thomas, 1910, inflated bullae characterize *G. nanus brockmani* Thomas (1910) and *G. watersi* (see Petter, 1975; Roche, 1976). Similarities are to those gerbils which have relatively uninflated bullae—*G. pusillus* and *G. harwoodi*.

From its description and published measurements (Thomas, 1901; Hollister, 1919; Roche, 1976), *G. harwoodi* seems to be very close to *G. bottai*, but my comparative material is insufficient (Table 1) to prove a synonymy of these; Roche (1976) emphasizes the darker coloration of *G. harwoodi* in contrast to *G. pusillus*, which is also true for *G. bottai*.

It cannot be excluded that some of the specimens listed by Yalden et al. (1976) as *G. ruberrimus* Rhoads, 1896 (which included *G. harwoodi* as a synonym), belong to *G. bottai*.

The above comparisons suggest regarding *G. stigmonyx* Heuglin, 1877, as a *nomen dubium* and uniting *G. luteolus* Thomas, 1901, and *G. harwoodi* Thomas, 1901, under the older name *G. bottai* Lataste, 1882, which would belong to the subgenus *Hendecapleura* as redefined by Schlitter and Setzer (1972).

Sennar (or in other spellings, Senar, Sennaar, Senaar) was an independent kingdom of the Funj, which was destroyed politically by the advance of Arabs into the Bilad As-Sudan (the country of the black). It stretched northward to Khartoum and comprised most of the Blue Nile Valley to the south, in what is now the Republic of the Sudan, and westward to the White Nile (that is, the Nile above Khartoum to Lake No) into the area of today's Kosti. There was a boundary with the Nilotic Shilluk tribe; the Nilotic place names in that area disappeared only at the end of the last century. After the fall of the Sennar kingdom, the modern town of Sennar was the capital of the region, but also had an alternative name—Makwar; the first Blue Nile Dam at Sennar was named Makwar Dam after its construction in the second decade of this century.

Customs and traditions changed only slowly; domestic pigs were kept and eaten a hundred years ago and were still offered for sale to Europeans in 1960. The name "Sennar" for a geographical region was gradually replaced by the Arabic designation "Gezira," meaning the island (between the two Niles). During the British rule, the Blue Nile Province was formed, and Sennar became a district.

To the early travellers and explorers, Sennar was but the region, and not a place or town. Bruce (1791) described the position of Sancaha as on the border between Sennar and Ethiopia. Eduard Rüppell, who explored in the northern Sudan, sent his hunter to collect along the Blue Nile; all this material now in the Senckenberg Museum is labelled "Sennar." This is also valid for other collections and has sometimes been used in a very liberal way, as for *Gazella dama ruficollis* (H. Smith, 1827) from Sennar, listed by Setzer (1956); there was never in recent times a *dama* gazelle to the east of the Nile.

Occasionally the meaning of Sennar remains completely obscure to its user; Elliot (1912) describes the distribution of *Papio cynocephalus* as Nubia, Central and East Africa in Sennar.

Many species were described from Sennar (compare list of synonyms in Setzer, 1956) and in most cases if not all, this has to be identified as *terra typica*, not as a *locus typicus*. If in the early descriptions of species from the Blue Nile region the habitat is given as Sennar, and other places which can be more precisely identified, like Sennar and Fazoglo (= Fazughli) for *Rhinopoma sennaariense* Fitzinger, 1866, preference should be given to the second habitat name as type locality (Kock, 1969), especially as there is no hill at Sennar where these bats could find a cave to shelter.

ACKNOWLEDGMENTS

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KARYOTYPE OF *GERBILLUS PYRAMIDUM* I. GEOFFROY (RODENTIA, GERBILLIDAE) FROM SENEGAL

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ABSTRACT

Gerbillus pyramidum is reported from Senegal for the first time. The external and cranial measurements and karyotype of the female specimen are presented.

INTRODUCTION

A large hairy-footed gerbil was collected for the first time in Senegal near M'Boro (15°12'N, 16°55'W), in December 1975 by W. Böhme, during a scientific expedition (for details of this excursion see Böhme, 1978).

This specimen is a large female; its dorsal fur is orange-fawn in color, but rather pale. The hairs of the middle of the back have a gray base; those of the sides are white. The belly is pure white. A dark line surrounds the eye; there is a white spot just behind the eye and another behind the ear. The vibrissae are pale or dark.

RESULTS

External measurements are given to the nearest millimeter. Cranial measurements were taken with a dial caliper and recorded to the nearest tenth of a millimeter. The bullae are measured as indicated by Ellerman and Morrison-Scott (1951), that is from the paraoccipital process to the anterior tip of the bulla. Length of feet includes the claws.

External and cranial measurements were as follows: head and body, 122; tail, 156; ear, 14; hind foot, 34; occipitonasal length, 34.8; greatest zygomatic breadth, 19.1; least interorbital constriction, 6.1; length of maxillary toothrow, 4.8; auditory bulla, 9.3.

The karyotype was prepared by the "air-drying" method and shows 40 chromosomes—18 pairs of biarmed chromosomes and one pair of small acrocentrics (Fig. 1). The two X-chromosomes are metacentrics. The FN is 78 arms.

DISCUSSION

According to Petter (1975), the morphological characters and the measurements are those of *Gerbillus pyramidum* I. Geoffroy, 1825. The karyotype (2N = 40) is closely related to those published by Matthey (1952), from Beni Abbes, Algeria, by Wharman and Zahavi (1955) also from Algeria, by Jordan et al. (1974) from Tunisia, and by Lay et al. (1975) from Morocco. These last authors still distinguished *Gerbillus pyramidum tarabuli*, with 2N = 40, from *Gerbillus pyramidum pyramidum*, whose karyotype, with 38 chromosomes, is similar to that described by Wassif et al. (1969) from Egypt.

The Senegalese specimen was collected in a very dry coastal area consisting of wind-blown sand dunes of quaternary origin; herpetologically these sand dunes are characterized by lizards with northern (Palearctic) affinities (for example, *Acanthodactylus dumerili, Scincus albofasciatus, Chalcides sphenopsiformis* and so on). The rather large measurements of the Senegalese specimen agree with those of the other specimens collected south of the Sahara (Rosevear, 1969; Setzer and Ranck, 1971). It presented the same morphological details as those described by Lay et al., 1975: "tympanic and

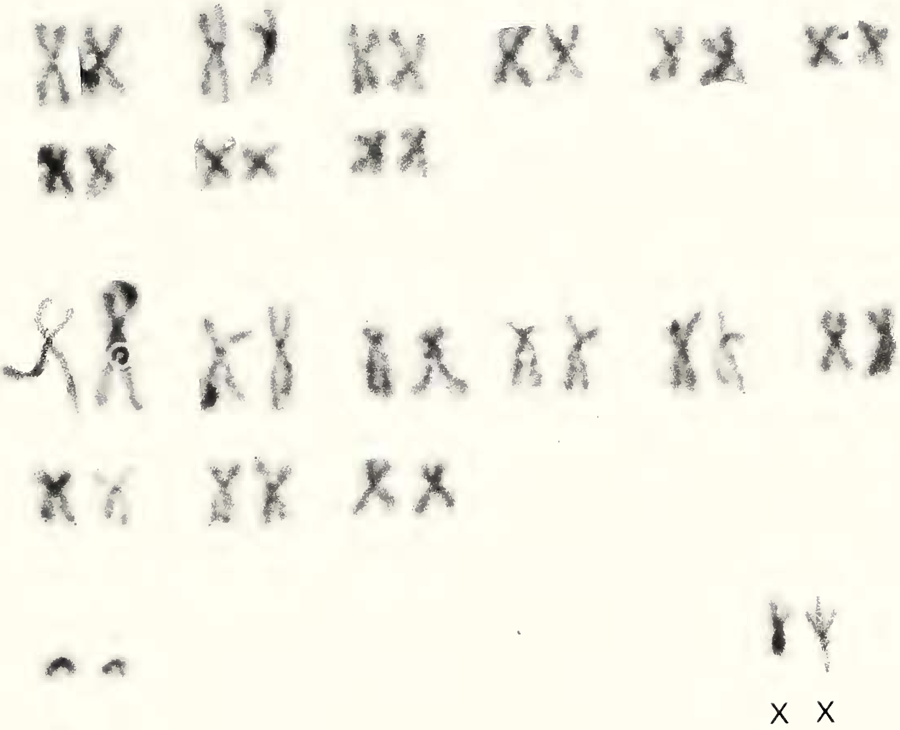

Fig. 1.—Karyotype of a female *Gerbillus pyramidum* from M'Boro, Senegal.

mastoid components of the auditory bullae are distinctly less voluminous in *G. pyramidum*, the anterior end of the basio-occipital contacts the medial walls of both tympanic bullae and is relatively narrower in the Algeria-Morocco sample; the posterior palatine foramina are shorter and more constricted; the nasal-frontal bone contact is broad in *G. pyramidum* and narrow in the Algeria-Morocco sample.''

This gerbil, whose chromosomes are nearly all metacentrics, and whose karyotype, the first known south of the Sahara, is homogenous with the other populations of *Gerbillus pyramidum* from Africa, seems to be particularly closely allied with the specimens from Morocco. A hypothesis is that these individuals have been derived from a single ancient population that existed throughout the Sahara; however the communication is now broken, as it is for *Mastomys* (Tranier, 1974). An extensive collection of *Gerbillus* from this area and other similar but distant areas would allow completion of this study.

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KARYOLOGICAL AND MORPHOLOGICAL COMPARISONS OF *LEMNISCOMYS STRIATUS* (LINNAEUS, 1758) AND *LEMNISCOMYS BELLIERI* VAN DER STRAETEN, 1975, FROM IVORY COAST (MAMMALIA: MURIDAE)

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ABSTRACT

The differences between two species of the *Lemniscomys striatus*-complex of Ivory Coast are described with the help of karyological, morphological, and biostatistical techniques. *Lemniscomys s. striatus* has a chromosomal set of 44, whereas *L. bellieri* has 2N = 56.

INTRODUCTION

Two forms of the *Lemniscomys striatus*-complex are known to occur in Ivory Coast. One we consider to be typical *Lemniscomys striatus*, the other is *Lemniscomys bellieri*.

The original description of *Lemniscomys striatus* by Linnaeus (1758) is so incomplete and vague that it can be matched to any of the known forms of the *striatus*-complex. Moreover the original type locality "India" mentioned by Linnaeus is clearly erroneous. Thomas (1911), in trying to solve this problem, concluded that the specimen described by Linnaeus probably came from Sierra Leone.

When we consider the geographic distribution of the *Lemniscomys striatus*-complex as it is actually known and that the original type-specimen undoubtedly came from a region not too far from the seashore, we have to conclude that the specimens of the forest-belt of the Ivory Coast are to be assigned to typical *Lemniscomys striatus*. This form lives in the clearings of the forest, at the fringes of the forest, in the cultivated areas near the villages, and in the more or less forested savannah.

In this publication we will discuss the biometrical and karyological differences, which enabled us to describe *Lemniscomys bellieri* as a new species (Van der Straeten, 1975*b*). As far as is known this new species inhabits the Guinean savannah (arborated and gras savannah) as well as the doka savannah of Ivory Coast and Ghana. In a forthcoming paper, we will show that *Lemniscomys bellieri* is related to *L. macculus* of eastern Africa.

In eastern Africa (more specifically northern and eastern Zaïre, southern Sudan, Ethiopia, Uganda, Rwanda, and Burundi) there coexists, just as in Ivory Coast, a bigger (*L. s. striatus* or *L. s. massaicus*) with a smaller (*L. macculus*) form of the *Lemniscomys striatus*-complex.

MATERIAL AND METHODS

For this study we were able to examine the very important collections made in Ivory Coast by our friend and colleague Dr. L. Bellier during the period 1963–1971. These collections were kindly made available to us by the O.R.S.T.O.M.

Out of this very important collection we studied 251 specimens of *Lemniscomys bellieri*, all of which were captured in Lamto (06°12′N; 04°58′W). The 395 specimens of *Lemniscomys s. striatus* we included in this study were obtained in Adiopodoumé (05°20′N; 04°08′W), Dabou (05°21′N; 04°26′W), Lamto, and Mopoyem (05°19′N; 04°30′W). All of this material will later be deposited in the Muséum National d'Histoire Naturelle (Paris-France) and in the Koninklijk Museum voor Midden-Afrika (Tervuren-Belgium). The complete list of the specimens is published in Van der Straeten (1975*a*).

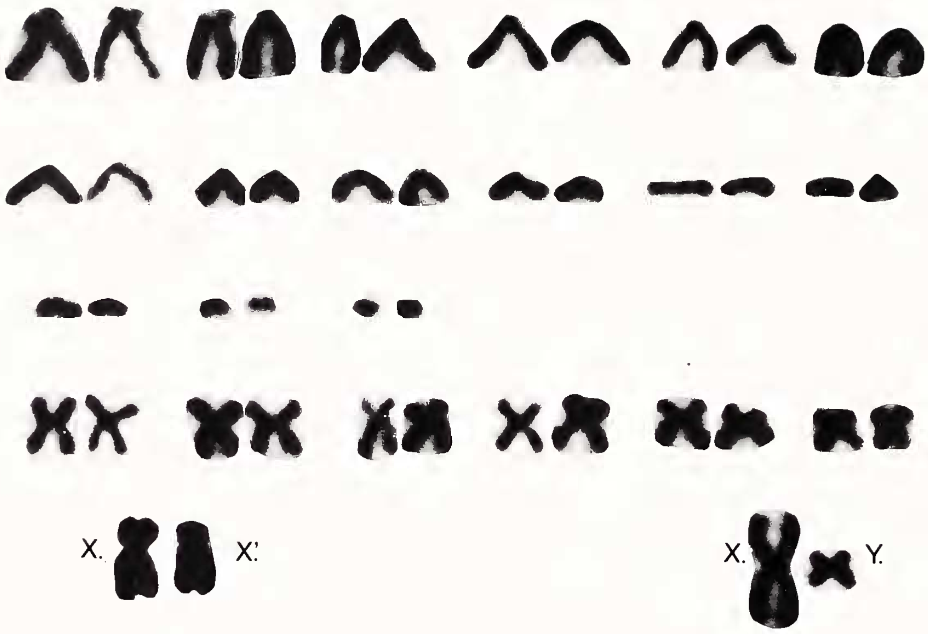

Fig. 1.—Karyotype of a male *Lemniscomys s. striatus* (coll. no. 846) and sex chromosomes of a female *L. s. striatus* (coll. no. 807).

The chromosome slides with the air-dried preparations were made in the Laboratoire d'Ecologie animale of the O.R.S.T.O.M. in Adiopodoumé, Ivory Coast, during February and March 1972. The eight specimens of *Lemniscomys bellieri* (six males and two females) were captured in Lamto and produced 74 (57 male and 17 female) countable mitoses spreads from which 12 (seven male and five female) were selected for measuring. All of the karyological results for *Lemniscomys striatus striatus* were obtained with five specimens (two males and three females) from Dabou and 10 (four males and six females) from Adiopodoumé. Together they produced 198 (62 males and 136 female) countable mitoses spreads, from which 55 (21 male and 34 female) were measurable. The following specimens in the Koninklijk Museum voor Midden-Afrika (collector numbers in parentheses) were those from which air-dried karyological preparations were made: *Lemniscomys bellieri*, Lamto (males—1275, 1276, 1282, 1331, 1334, 1339; females—1266, 1279); *Lemniscomys s. striatus*, Adiopodoumé (males—29, 569, 1010, 1104; females—119, 568, 1145, 1176, 1312, 1386); *L. s. striatus*, Dabou (males—830, 846; females—807, 831, 848).

Skull measurements and statistical methods are the same as used in former studies (Van der Straeten and Van der Straeten-Harrie, 1977; Van der Straeten and Verheyen, 1977). The 18 measurements which were used are enumerated in Table 3. The external measurements were copied from the labels. The hind foot length was measured with the nail.

The air-dried preparations were made following the slightly modified method of Hsu and Patton (1969). The chromosomal measurements were taken with a curvimeter; each measurement was taken 10 times, after which the mean was calculated. These data were used to pair the chromosomes. This pairing procedure was executed with an IBM 1130 computer and a FORTRAN program.

RESULTS

Description of Karyotypes

Lemniscomys striatus striatus.—Of the 198 counted mitoses spreads, 78.8% have $2N = 44$ and $NF = 72$. The karyotype is composed of eight pairs of telocentric chromosomes, seven pairs of subtelocentric chromosomes, six pairs of metacentric chromosomes, and 1 pair of sex chromosomes XX' or XY (see Figs. 1 and 2). The X-chromosome is the largest metacentric chromosome; the X' the only submetacentric one. The Y-chromosome could not be identified with absolute certainty but we suppose that it is the smallest metacentric chromosome.

It is remarkable that in the females the sex chromosomes form a heterogenic pair. The difference between the X and X' chromosome is due to a difference in length of the short arms.

In some of the telocentric chromosomes a very short additional arm can be observed; it is possible that a number of them should be considered to be acrocentric. However the quality of the preparation

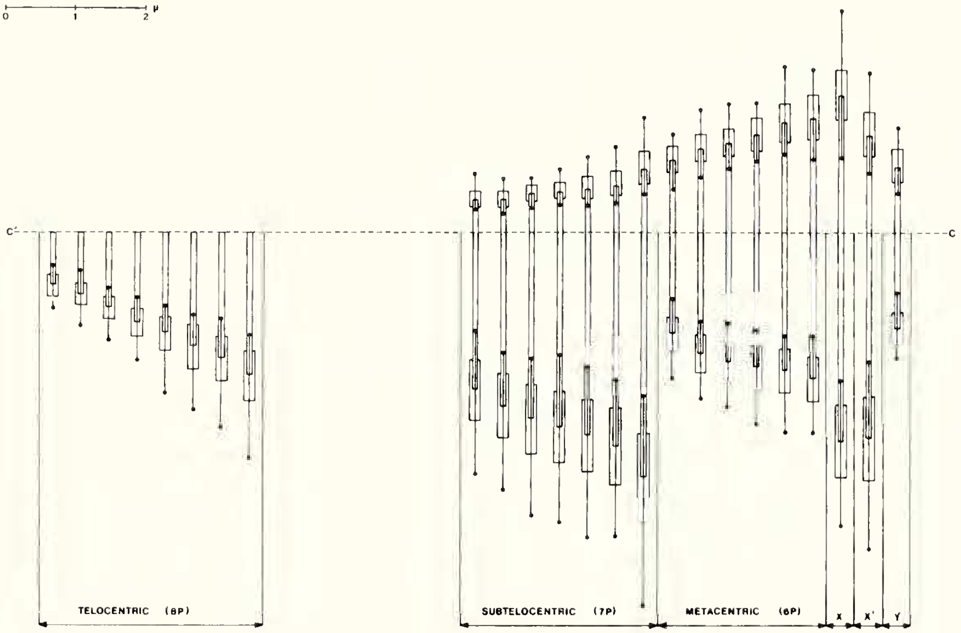

Fig. 2.—Graph showing karyotype of *Lemniscomys s. striatus*. Mean, mean ± standard deviation, and range are indicated for each chromosome.

and the photographs did not allow further investigation.

With the exception of the sex chromosomes we could not find a difference between the male and female karyotype.

Lemniscomys bellieri.—Of the 74 studied mitoses spreads, 55.4% show a diploid number of 56 (= 2N) and a fundamental number of 78 (=NF). The karyotype is composed of 17 pairs of telocentric chromosomes, seven pairs subtelocentric chromosomes, three pairs metacentric chromosomes, and one pair of sex chromosomes XX' or XY (see Figs. 3 and 4).

In this species the X-chromosome is also the largest metacentric of the karyotype and the X' chromosome is submetacentric. The Y-chromosome is the second longest metacentric or is perhaps submetacentric. Here also the sex chromosomes of the female form a heterogenic pair XX'.

There is a certain similarity between the karyotypes of *L. striatus striatus* and *L. bellieri* when we

Table 1.—*Eigenvalues of the canonical transformation with test of significance.*

No.	Eigenvalue	Relative importance (%)	Chi-square	Degrees of freedom	Probability
1	373.792	81.7	872.046	76	1.000
2	61.164	13.4	269.359	54	1.000
3	14.264	3.1	83.239	34	0.999
4	8.260	1.8	31.069	16	0.987

Table 2.—*Eigenvectors of 19 variables for the first three canonical variates.*

Variable code	1	2	3
HL	0.5831	0.1932	−0.3783
GRLE	−0.9375	−0.4675	0.3525
PRCO	0.4559	3.8381	−0.2940
HEBA	0.3818	−2.6529	0.4863
HEPA	0.7462	−0.4103	0.9431
PAF	−0.0886	1.1638	0.5596
D1A1	−0.3928	−3.4485	−1.6678
D1A2	−0.6140	0.5533	−0.6217
INT	2.2791	−0.6067	1.6093
ZYG	0.2112	0.4286	0.9798
UPTE	0.0120	−1.9578	−0.2864
UPDE	−0.7466	1.6011	1.4716
M^1	4.3813	−1.5595	−13.0248
ZYPL	−0.1754	0.2801	−0.8379
BNAS	−0.5152	−1.2736	−2.1432
LNAS	1.0952	0.2441	−0.5363
LOTE	0.3778	0.7545	−0.1532
BUL	−4.1282	−0.0960	−1.4002
BRCA	0.4681	−0.8785	−0.0589

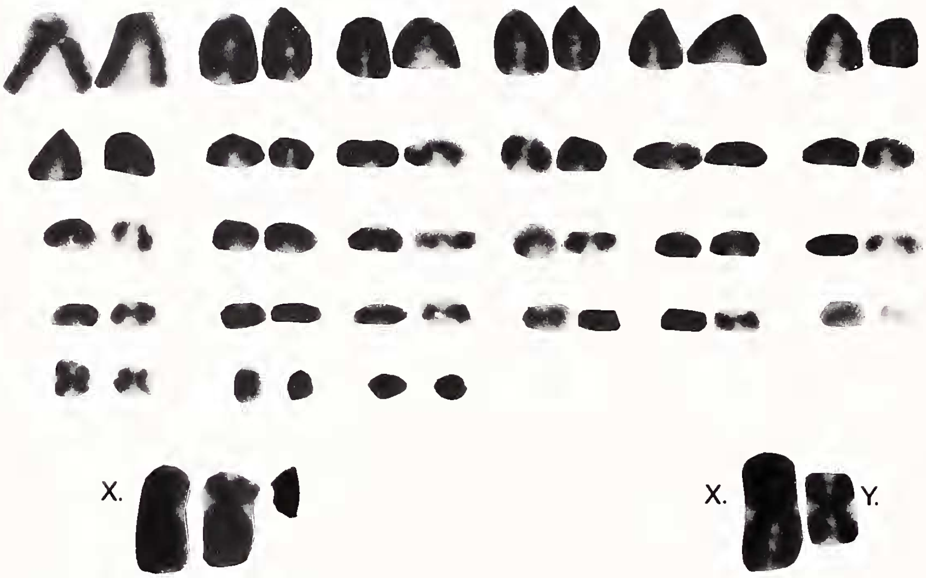

Fig. 3.—Karyotype of a male *Lemniscomys bellieri* (coll. no. 1275) and sex chromosomes of a female *L. bellieri* (coll. no. 1279).

consider the X-chromosome, the X′-chromosome, and the seven pair of subtelocentric chromosomes.

Canonical Analysis

For the canonical analysis, we used 397 specimens collected in four localities and divided as follows in five groups: 1, *Lemniscomys s. striatus*, Adiopodoumé (25 specimens); 2, *Lemniscomys s. striatus*, Dabou (74); 3, *Lemniscomys s. striatus*, Mopoyem (88); 4, *Lemniscomys s. striatus*, Lamto (43); 5, *Lemniscomys bellieri*, Lamto (167).

We based this analysis on 18 skull measurements (see Table 2) and one external measurement (the hind foot length). The four canonical variates differ significantly from O. The first contains 81.7% of the total variation; the first and second together represent 95.1% of the total variation. In Table 1 we give the eigenvalues of the canonical transformation and in Table 2 the eigenvectors of the 19 variables for the first three canonical variates. Starting from these eigenvectors a graphical representation is made. For each group the center and the most extreme values are indicated by a polygonal delimitation. In Fig. 5 we give the graphical representation of the first and second canonical variate.

The first canonical variate shows a very clear division between two groups—*Lemniscomys bellieri* and *L. s. striatus*. The overlap is very small. The second canonical variate separates *Lemniscomys s. striatus* in two subgroups depending upon their geographic origin; one subgroup includes the specimens from Adiopodoumé-Dabou and the other includes animals from Lamto-Mopoyem. The overlap, however, is extensive. The third canonical variate gives no further information.

When we consider the same species but now with the specimens grouped in age-classes we obtain similar results. Indeed, the first canonical variate separates *L. bellieri* from *L. s. striatus*, whereas the second variate separates the specimens on the basis of age.

Finally, if we consider the same species but now grouped following age and collecting locality similar results are obtained. The first variate separates *bellieri* from *striatus* and the second one separates the specimens according to age. In the second variate the differences between the subgroups Adiopodoumé-Dabou and Lamto-Mopoyem remain when one compares animals of comparable age groups.

Taxonomical Characters and Discrimination Analysis

Lemniscomys bellieri is in its overall measurements clearly smaller than *L. s. striatus* (Table 3). This is especially true for the hind foot length of the adults—*L. bellieri* 25.4 mm (23.0–27.0); *L. s. striatus* 26.0 mm (24.0–31.0).

Both species differ also strikingly in their dorsal

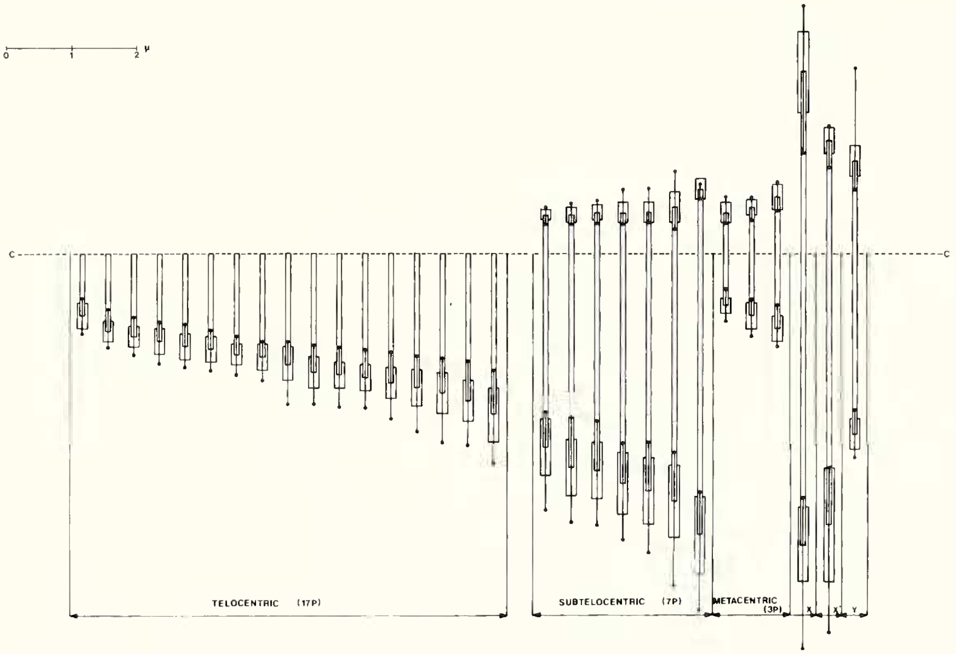

Fig. 4.—Graph showing karyotpye of *Lemniscomys bellieri*. Mean, mean ± standard deviation, and range are indicated for each chromosome.

pelage pattern. *L. s. striatus* has on both sides of its black mediodorsal stripe, eight light longitudinal stripes, each of which on closer examination is composed of a row of individualized spots (more to the eastern part of Africa-Zaïre and Ethiopia—we find specimens of *L. s. striatus* where the individual spots show the tendency to blend into a set of continuous longitudinal light stripes). *Lemniscomys bellieri* also shows eight light longitudinal stripes on each flank and a sharply defined black mediodorsal line. It must be noted, however, that only the third, fourth, and fifth stripes are clearly outlined. The individual spots are not neatly defined and melt more or less away in the darker background, resulting in an even more fuzzy dorsal pattern.

Lemniscomys s. striatus is craniometrically larger than *L. bellieri* and M_1 of *L. s. striatus* has mostly an Sm, which is generally absent in *bellieri*.

Notwithstanding all these morphological and metrical characters, a correct determination can give some difficulties when one examines only a skull. For this reason, we calculated two discriminant functions. Because these functions are based on museum material exclusively from Ivory Coast, it is obvious that the proposed functions can only be used on Ivory Coast specimens.

For the first discriminant function we used all of the 18 cranial measurements as well as the hind foot length (including nail). The data for 229 specimens of *L. s. striatus* were included as well as the data for 167 specimens of *L. bellieri*. The first discriminant function is calculated as follows: $K = 2.416 \times HL + 7.517 \times INT + 16.284 \times M^1 + 2.553 \times LNAS - 16.525 \times BUL - 70.229$. If $K > 0$, then we are dealing with *L. s. striatus*, if $K < 0$, then it is *L. bellieri*. The chance of misidentification is 3.5%.

The second discriminant function concerns only the cranial measurements and was computed with the same data as the first. It is calculated as follows: $K = 4.320 \times HEPA - 3.985 \times DIA\ 2 + 8.427 \times INT + 2.772 \times LNAS - 13.470 \times BUL - 23.793$. If $K > 0$ then the specimen is a *L. s. striatus*; if $K < 0$, it is a *L. bellieri*. The chance of misidentification here is 6.2%

DISCUSSION AND CONCLUSIONS

There can be no doubt that two species of the *Lemniscomys striatus*-complex exist in the Ivory Coast—the smaller *L. bellieri* and the larger *L. striatus striatus*. It was possible to describe *L. bel-*

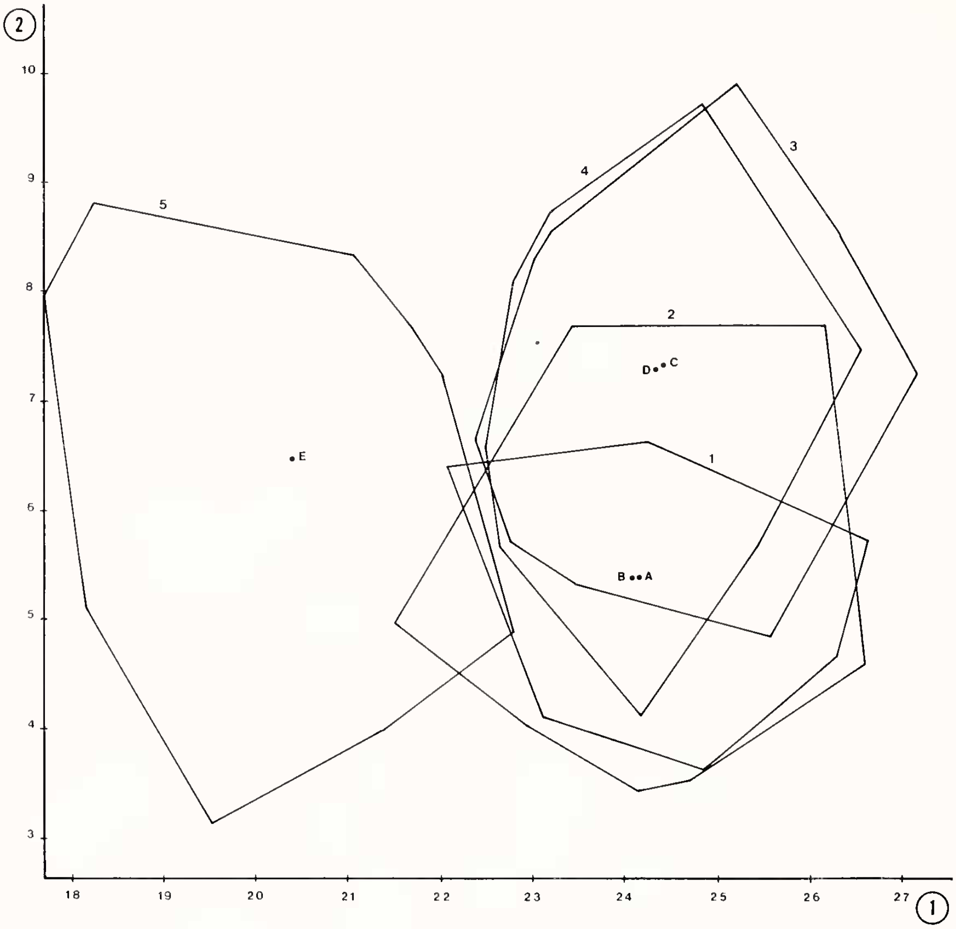

Fig. 5.—Canonical analysis: canonical means (solid circles) and extreme limit of each cloud of points; canonical variates I (abscissa) and II (ordinate); 1 (A) *Lemniscomys s. striatus* from Adiopodoumé, 2 (B) *L. s. striatus* from Dabou, 3 (C) *L. s. striatus* from Mopoyem, 4 (D) *L. s. striatus* from Lamto and 5 (E) *L. bellieri* from Lamto.

lieri as a new species because we are in the possession of a very important series of skins and skulls, which allowed a biostatistical approach, and we made air-dried preparations for karyological study.

In all of the older museum collections we were able to examine, we found only two specimens of *L. bellieri* (British Museum Natural History, 23.2.3.42 and 23.2.3.43, collected in 1922 by Lowe and Hardy in Béoumi, Ivory Coast). Both animals were labeled as belonging to the species *L. striatus*. Rosevear (1969), who studied these specimens, noted that they are smaller and show an aberrant dorsal pattern. He explained both characteristics by stating that the specimens are juveniles, which is clearly an error because the teeth and the skull sutures show that we are dealing with adults.

The dorsal stripe pattern of *L. bellieri* shows a certain similarity with that of *L. striatus venustus*. However, in all other respects both are very different. Indeed, the latter is the largest form of the *Lemniscomys striatus*-complex, whereas *bellieri* is the smallest.

The karyotypes of *L. s. striatus* and *L. bellieri* show certain similarities in the X and X′ chromosome as well as in the seven pairs of subtelocentric chromosomes. Matthey (1959) first described the chromosomes of *L. striatus*. The results of his study were 2N = 48, four metacentrical chromosomes, and NF difficult to establish but probably around 60. It is probable that this specimen belongs to an East African form of *L. striatus*. Regrettably, skin and skull were not prepared so that an exact determination of his specimen will remain impossible.

Table 3.—*Measurements in mm of adult* Lemniscomys. *Number of specimens, mean, and range are given from left to right for each species.*

Variable code	Description	*L. s. striatus*	*L. bellieri*
HB	Head and body length	331; 118.1 (61.0–170.0)	220; 109.8 (91.0–127.0)
TL	Length of tail	300; 114.1 (30.0–143.0)	186; 113.3 (70.0–134.0)
HL	Length of hind foot + nail	340; 26.0 (24.0–31.0)	211; 25.4 (23.0–27.0)
EL	Length of ear	317; 15.2 (10.0–18.0)	203; 15.9 (13.0–19.0)
GRLE	Greatest length of skull	317; 29.63 (23.30–33.35)	223; 28.25 (24.35–31.30)
PRCO	Prosthion—condylion	346; 26.66 (23.10–30.10)	240; 25.31 (22.35–27.75)
HEBA	Henselion—basion	346; 22.83 (19.10–25.70)	230; 21.47 (18.75–23.70)
HEPA	Henselion—palation	349; 12.27 (10.40–13.70)	244; 11.50 (10.20–12.85)
PAF	Length of palatal foramina	349; 5.83 (4.85–6.85)	240; 5.53 (4.80–6.30)
DIA1	Length of diastema	349; 7.17 (5.75–8.50)	242; 6.72 (5.80–7.75)
DIA2	Distance between the anterior border of the alveole of M^1 and the edge of upper incisor	331; 7.70 (6.20–9.20)	225; 7.21 (6.15–8.20)
INT	Interorbital breadth	349; 4.87 (4.30–5.55)	241; 4.42 (3.85–5.05)
ZYG	Zygomatic breadth on the zygomatic process of the squamosum	328; 13.54 (11.95–15.30)	229; 12.82 (11.20–14.40)
UPTE	Length of upper cheekteeth	353; 5.35 (4.60–5.90)	250; 5.11 (4.60–5.65)
UPDE	Breadth of upper dental arch	330; 6.06 (5.20–6.95)	233; 5.82 (5.15–6.50)
M^1	Breadth of M^1	355; 1.66 (1.40–1.85)	248; 1.61 (1.45–1.75)
ZYPL	Breadth of zygomatic plate	350; 3.56 (2.95–4.20)	242; 3.35 (2.65–4.10)
BNAS	Greatest breadth of nasals	329; 3.34 (2.70–4.30)	230; 3.16 (2.70–3.65)
LNAS	Greatest length of nasals	317; 11.59 (9.30–13.60)	223; 10.64 (8.55–12.20)
LOTE	Length of lower cheekteeth	350; 5.09 (4.50–5.55)	251; 4.88 (4.45–5.45)
BUL	Length of auditory bulla	339; 4.94 (4.25–5.60)	239; 5.08 (4.55–5.70)
BRCA	Braincase breadth	345; 12.15 (11.05–13.00)	240; 11.69 (10.50–12.90)

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REVISION OF THE GENUS *SACCOSTOMUS* (RODENTIA, CRICETOMYINAE), WITH NEW MORPHOLOGICAL AND CHROMOSOMAL DATA FROM SPECIMENS FROM THE LOWER OMO VALLEY, ETHIOPIA

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ABSTRACT

Based upon new records of *Saccostomus* from southwestern Ethiopia, a revision of the genus is considered. Morphometric and karyological evidence indicate two species should be recognized—*S. campestris* from southern Africa and *S. mearnsi* from eastern Africa.

INTRODUCTION

Seven rodents of the genus *Saccostomus* were collected during the summer of 1973 in the Lower Omo Valley, Ethiopia, during a paleontological expedition directed by Y. Coppens. These individuals are noteworthy because of their shaggy fur, uniformly brownish-gray in color, and consisting of long, soft, and silky hairs. The belly of these specimens is paler than the back, but still definitely grayish, unlike the forms from southern Africa with their pure white belly and their sleek but less shaggy fur.

RESULTS AND DISCUSSION

Table 1 presents the main external and cranial measurements for the specimens collected in the Lower Omo Valley, Ethiopia; three specimens from the British Museum, one from Ethiopia (reported by Yalden et al., 1976) and two from Uganda; three specimens from the Museum National d'Histoire Naturelle (MNHN) de Paris with southern African origin, one of which is the specimen studied by Matthey (1958). The measurements published by Roche (1976) for a specimen from Somalia are also reported here. External measurements are given to the nearest millimeter; cranial measurements were taken with a dial caliper and reported to the nearest tenth of a millimeter.

The specimens from northeast Africa (Uganda, Ethiopia, and Somalia) have a gray belly, a long ear (more than 20 mm), a long tail (more than 50 mm), and a long maxillary toothrow (more than 5.0 mm). The three southern specimens from the MNHN have a white belly, a short ear (less than 20 mm), a short tail (40 mm), and a short maxillary toothrow (less than 5.0 mm). The same characters are present on all the specimens from southern Africa that I studied in the British Museum, particularly the cotypes of *Saccostomus campestris* Peters.

The karyotypes were observed for two individuals in 1973 by the "squash" method as described by Matthey (1958), and for two others in 1976–1977 by the "air-drying" method. The slides are not very easily interpreted, but the chromosome number was always between 40 and 42, never exceeding this last number, in more than 20 metaphases observed (Fig. 1). Ford and Hamerton (1956) published a karyotype of 2N = 44 for an individual of unknown origin, but Matthey (1958) considers that it is difficult material to interpret and that the number of chromosomes for *Saccostomus campestris* is 2N = 46, as he personally observed on a specimen collected in the Cape Province, South Africa.

Ellerman (1941) thought that there was only one species of *Saccostomus*—*S. campestris* Peters. Misonne (1968) agreed with him, but Roche (1976) thought that his specimen from Somalia was closely related to the other specimens from the "north," and different from the southern African *Saccostomus campestris*. I think that Ethiopian specimens, which are different by their morphological characters, by their measurements, and by their karyotype, represent a distinct species together with all the *Saccostomus* from the north of this area in Africa (Ethiopia, Uganda, Somalia, and Kenya). Prior to the revision of Ellerman (1941), different species had been described from these countries as follows: *Saccostomus umbriventer*, Miller, 1910; *Saccosto-*

Table 1.—*Selected external and cranial measurments of* Saccostomus *examined from the Museum National d'Histoire Naturelle, Paris, and the British Museum (Natural History), London.*

Number	Sex	Origin	Head and body	Tail	Hind foot	Ear	Oc-cipito-nasal length	Zygo-matic breadth	Inter-orbital con-stric-tion	Upper molar row	Bulla	Obser-vations
1974—54	♂	Omo, Ethiopia	140	50	24	20	32.0	17.2	4.6	5.6	6.2	Gray belly
1974—55	♀	Omo, Ethiopia	144	56	22	23	35.1	19.1	4.4	5.6	7.3	Gray belly
1974—56	♀	Omo, Ethiopia	149	70	25	25	34.0	18.8	4.5	5.9	7.0	Gray belly
814	♂	Omo, Ethiopia	150	81	23	22	36.7	19.6	4.9	5.9	6.9	Gray belly
1977—1	♀	Omo, Ethiopia	137	58	22	20	36.2	19.5	4.5	7.0	7.0	Gray belly
1977—2	♀	Omo, Ethiopia	141	58	23	23	34.9	19.4	4.5	6.3	6.9	Gray belly
1977—3	♀	Omo, Ethiopia	153	67	24	24	36.2	19.5	4.4	6.2	6.2	Gray belly
BM 46.740	♀	Karamoja, Uganda	140	50	22	20	32.2	17.0	4.4	5.9	6.5	Gray belly
BM 71.450	♂	Karamoja , Uganda	—	—	—	—	34.5	18.0	4.7	5.8	5.9	Gray belly
BM 71.451	♂	Karamoja, Uganda	117	69	19.4	20.2	31.2	17.4	4.3	5.6	7.2	Gray belly
BM 73.490	♀	Maji, Ethiopia	116	64	22	21	—	—	—	—	—	Gray belly
3047—MF	♀	Giohar, Somalia	144	72	23	20	35.3	17.3	4.1	6.2	—	Gray belly
1958—226	♂	Transvaal, R.S.A.	125	40	22	17	35.7	17.8	4.7	4.5	8.0	White belly
1964—56	♂	Rhodesia	118	40	19	16	30.8	—	4.3	4.6	6.0	White belly
1969—57	♀	Rhodesia	122	40	19	17	32.4	—	4.5	4.3	6.4	White belly

Table 2.—*Means, standard errors, and standard deviation of the lengths of the tail, the ear, and the upper molar row from different populations from the American museum collections. The measurements of the upper molar row were made by the author and permit statistical tests on the homogeneity of the different populations. The two groups are homogeneous and each different from the other. The specimens from Tanzania are different from the two groups, but their characters are reported to the second.*

Origin	Number of specimens	Length of the tail		Length of the ear		Length of the upper molar row		Significance
		Mean ± standard error	Standard deviation	Mean ± standard error	Standard deviation	Mean ± standard error	Standard deviation	
Northern Rhodesia (AMNH)	63	47.5 ± 0.7	5.39	18.2 ± 0.1	0.76	4.68 ± 0.03	0.27	
Angola (AMNH)	5	46.4 ± 2.5	5.68	16.0 ± 1.0	1.40	4.44 ± 0.07	0.16	F = 0.92 < 1
Bechuanaland (AMNH)	17	42.8 ± 0.8	3.51	17.2 ± 0.4	1.63	4.57 ± 0.06	0.23	
Nyasaland (AMNH)	23	39.3 ± 1.1	5.13	16.4 ± 0.2	0.86	4.57 ± 0.03	0.14	
Southern Rhodesia (AMNH)	13	45.3 ± 2.3	8.0	16.0 ± 0.6	1.87	4.61 ± 0.04	0.15	homogeneous
South West Africa (AMNH)	5	48.1 ± 3.1	6.97	18.5 ± 0.8	1.70	4.69 ± 0.28	0.63	population
Transvaal (USNM)	13	46.2 ± 2.2	8.12	17.7 ± 0.4	1.42	4.68 ± 0.07	0.25	
Bechuanaland (USNM)	14	44.1 ± 1.1	5.13	16.9 ± 0.3	1.21	4.71 ± 0.05	0.21	
Mozambique (Gaza) (USNM)	13	44.0 ± 1.4	4.59	17.3 ± 0.3	0.90	4.49 ± 0.05	0.18	
Mozambique (Tete) (USNM)	14	43.1 ± 0.9	3.16	16.9 ± 0.2	0.90	4.48 ± 0.05	0.20	
Nyasaland (MCZ)	5	34.5 ± 1.9	3.87	17.7 ± 0.4	0.95	4.17 ± 0.08	0.18	
								t = 16.66 t > 1.96 significant difference
Uganda (AMNH)	3	77.7 ± 10.7	18.40	—	—	6.08 ± 0.07	0.14	F = 0.67 < 1
Kenya (USNM)	25	61.4 ± 1.13	5.54	19.4 ± 0.3	1.70	5.94 ± 0.05	0.27	homogeneous
Kenya (MCZ)	4	56.7 ± 4.8	9.71	22.0 ± 0.0	0.00	5.86 ± 0.06	0.11	population
Omo (MNHN)	7	62.9 ± 3.9	10.46	22.4 ± 0.7	1.90	6.07 ± 0.18	0.49	
Tanganyika (AMNH)	29	48.8 ± 1.2	7.2	—	—	5.38 ± 0.04	0.21	significant difference

Fig. 1.—Karyotype of *Saccostomus mearnsi* from Omo Valley, Ethiopia.

mus mearnsi, Heller, 1910; *Saccostomus isiolae*, Heller, 1912; *Saccostomus cricetulus*, Allen and Lawrence, 1936. The holotypes of these species are deposited in the Smithsonian Institution, Washington, D.C., and at the Museum of Comparative Zoology, Harvard University.

The four species are closely related. The first described is *S. mearnsi*, the holotype of which is an adult male in good condition (better condition than *S. isiolae*, but younger than *S. umbriventer*, which is a very old female). *S. cricetulus* is not very different and when described by G. M. Allen and B. Lawrence they thought that the four species might be the same (Allen and Lawrence, 1936). I think that *Saccostomus mearnsi* is the available name for the northeastern species of *Saccostomus* characterized by a gray belly, a long tail (more than 49.0 mm), a large ear (more than 19.0 mm), a long maxillary toothrow (more than 5.0 mm), and a karyotype of 2N = 40–42 chromosomes.

Table 2 shows the means of the length of the tail, the ear, and the upper molar row for a group of specimens from the American Museum of Natural History, New York, from the United States National Museum, Washington, D. C., and from the Museum of Comparative Zoology, Harvard, collected in different countries of eastern and southern Africa. It shows the difference between the specimens from Zambia (Northern Rhodesia), Angola, Botswana (Bechuanaland), Malawi (Nyasaland), Zimbabwe (Southern Rhodesia), Transvaal, and Mozambique on one hand and from Tanzania, Uganda, Kenya, and Ethiopia on the other hand. The specimens from Kijungu, Tanzania, are referred to *S. mearnsi*, but they are a bit smaller than the individuals from the other northeastern countries, and statistically significantly different. Their karyotype is unknown.

An hypothesis to test is whether the division between the two species is the Rift Valley. Furthermore, it would be very interesting to collect some specimens in southern Tanzania or in northern Mozambique to test the possibility of speciation according to the latitude in this region.

SUMMARY

Two different species of *Saccostomus* are recognized—*S. campestris* from southern Africa, characterized by a white belly, a short ear (less than 19 mm), a small tail (less than 49 mm), a short upper molar row (less than 5.0 mm) and a karyotype of 2N = 46 chromosomes; *S. mearnsi* from eastern Africa, characterized by a gray belly, a large ear, a long tail, a long upper molar row and a karyotype of 2N = 40–42 chromosomes.

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TAXONOMIC REVIEW OF THE FAT MICE (GENUS *STEATOMYS*) OF WEST AFRICA (MAMMALIA: RODENTIA)

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ABSTRACT

Data from specimens of West African taxa of *Steatomys* were subjected to univariate and multivariate statistical analyses. Geographic and nongeographic variation were analyzed based upon an examination of 385 conventional museum specimens. From the results of the analyses, three species of *Steatomys* are recognized in West Africa. *Steatomys cuppedius*, a small monotypic species, occurs in the Sahel and Sudan Savanna zones of West Africa. *S. caurinus* exhibits geographic variation; two subspecies are recognized, one of which is described as new. *S. jacksoni* is retained as a unique species known only by the holotype from Ghana. Both *S. caurinus* and *S. cuppedius* exhibit a high degree of variation with age. Geographic distributions of the West African taxa are plotted based upon specimens examined and literature records.

INTRODUCTION

Fat mice of the genus *Steatomys* are members of the rodent family Muridae and together with the genera *Dendromus*, *Prionomys*, *Dendroprionomys*, *Leimacomys*, *Deomys*, and *Malacothrix* are included in the subfamily Dendromurinae. The phylogenetic affinities of the genera of this subfamily are little understood and the taxonomic relationships of the many described taxa are poorly known. Geographically, genera of this subfamily are distributed throughout subsaharan Africa in habitats ranging from subdesert to forest.

Species of the genus *Steatomys* occur throughout subsaharan Africa in habitats ranging from subdesert to degraded forest or forest edge. Generally, however, they are found in savannah. In spite of their widespread occurrence, specimens of the genus are not often taken because they do not readily enter any type of traps. In areas where individuals can be captured by hand at night or dug from their burrows, significant samples are being accumulated.

Initially, specimens were few and wide hiatuses existed between samples. During the last half of the nineteenth and early part of the twentieth centuries, individuals from each locality were usually described as a new taxon. There have been two major listings of the taxa in the genus. Allen (1939) listed 18 species with 26 subspecies, whereas Ellerman (1941) gave 18 species with 24 subspecies, some of which differed from Allen's list.

Three species of *Steatomys* have been described from West Africa—*S. caurinus* Thomas, 1912, from Panyam, Nigeria; *S. cuppedius* Thomas and Hinton, 1920, from Farniso [=Panisau], Nigeria; *S. jacksoni* Hayman, 1936, from Wenchi, Ghana, Allen (1939), Ellerman (1941), and Rosevear (1969) considered these three taxa to be distinct species, based generally on the original descriptions. In a recent provisional checklist of the genus, Coetzee (1977) listed both *S. caurinus* and *S. jacksoni* as subspecies of *S. pratensis* Peters, 1846, and *S. cuppedius* as a subspecies of *S. parvus* Rhoads, 1896. Both *S. pratensis* and *S. parvus* were considered by Coetzee (1977) to be widespread savannah-occurring Panafrican species. However, he has admitted to perhaps oversynonymizing the nominal taxa in his provisional checklist, wherein he recognized three species in the genus.

Relationships of the three West African forms to other species within the genus in the remainder of Africa is beyond the scope of the present study. A short review of described forms, which might occur sympatrically or parapatrically with these three taxa follows. *Steatomys opimus* Pousargues, 1894, originally described from material from the region now included in the Central African Empire, is found in degraded forest and woodland savannah in central Africa (Coetzee, 1977). Because it is known to occur in the Cameroons, it might therefore also occur in the southern parts of West Africa, at least in southern Nigeria. A large species (greatest length of skull above 30), *Steatomys opimus*, is considered by Coetzee (1977) to be only subspecifically distinct from *S. pratensis*, a more geographically widespread species described originally from southern Africa. Three additional species occur in the Sudan (Setzer, 1956)—*S. aquilo, S. gazellae,* and *S. thomasi.* Coetzee (1977) also synonymized *S. aquilo* and *S. gazellae* with *S. parvus*, and *S. thomasi* with *S. pratensis*.

The purpose of this study was to examine the systematic relationships of the nominal taxa of the genus *Steatomys* in West Africa, based on sizeable unreported collections in the Smithsonian Institution, Washington, D.C. Here West Africa is considered to be that portion of Africa west of the Nigerian border and south of the Sahara. This geographic limitation is not the same as that used by Rosevear (1965, 1969) who included those parts of Cameroon west of the Sanaga River.

MATERIALS AND METHODS

Conventional museum skins and skulls of 385 specimens of the genus *Steatomys* from West Africa were examined. All of the holotypes of western African taxa were examined by both authors. Five external and 14 cranial measurements were recorded, in millimeters, from nearly all specimens examined. External measurements were listed from the specimen labels; cranial measurements were taken with dial calipers. Definitions of these cranial measurements are given below:

Greatest length of skull.—Greatest distance from the anterior edge of the nasal bones to the posteriormost edge of the occipital bone.

Condylobasal length.—Greatest distance from the anteriormost projection of the premaxilla between the incisors to the posterior edge of the occipital condyles.

Zygomatic breadth.—Greatest distance across zygomatic arches at right angles to longitudinal axis of cranium.

Interorbital breadth.—Least distance across interorbital constriction.

Rostral breadth.—Least distance across the rostrum immediately anterior to the zygomatic plate.

Oblique length of bulla.—Greatest oblique length of auditory bulla, taken from a point adjacent to the paraoccipital process to the anteriormost edge of bulla.

Greatest length of bulla.—Greatest oblique length of bulla taken from the posterior edge of mastoidal bulla to the anteriormost edge of auditory bulla.

Length of maxillary toothrow.—Least distance from the anterior edge of alveolus of M^1 to posterior edge of the alveolus of M^3.

Breadth across upper molars.—Least distance, measured at right angles to the longitudinal axis of the skull, from the widest point on the labial edge of the crowns of M^1 in each maxillary toothrow.

Length of anterior palatal foramen.—Greatest distance from anterior edge to the posterior edge of the anterior palatal foramen.

Length of posterior palatal foramen.—Greatest distance from the anterior edge to the posterior edge of the posterior palatal foramen.

Length of diastema.—Greatest distance from the posterior edge of the alveolus of the incisors to the anterior edge of the alveolus of M^1.

Height of skull.—Greatest height of skull (taken perpendicular to the horizontal plane of skull when placed on a microscope slide).

Length of mandibular toothrow.—Least distance from the anterior edge of the alveolus of M_1 to posterior edge of the alveolus of M_3.

Univariate statistical analyses were performed on an IBM 360 computer at Carnegie-Mellon University, Pittsburgh, and multivariate statistical analysis on an IBM 370 computer at Texas Tech University, Lubbock. Univariate analyses of secondary sexual, age, and individual variation were performed using the UNIVAR program developed and published by Power (1970). Standard statistics (mean, range, standard deviation, standard error, variance, and coefficient of variation, among others) are generated by this program. In the event of two or more groups being compared, a single-classification analysis of variance (ANOVA) to test for significant differences between or among means is employed. When means were found to be significantly different, the Sums of Squares Simultaneous Test Procedure (SS-STP) was used to determine maximally nonsignificant subsets.

Multivariate statistical analyses were performed using the Numerical Taxonomy Systems (NT-SYS) package developed by F. J. Rohlf, R. Bartcher, and J. Kishpaugh at the University of Kansas. In these analyses the OTUs were grouped localities (geographical samples) and the values used for each measurement were arithmetic means for the measurement. Matrices of Pearson's product-moment correlation and taxonomic distance coefficients were computed. Cluster analyses were performed using the unweighted pair-group method using arithmetic averages (UPGMA) on correlation and distance matrices, and phenograms were generated for both. Only the distance phenogram is given as it gave larger coefficients of cophenetic correlation and the results of the distance phenogram also agree more closely with other analyses. Three principal components were extracted from the matrix of correlations, and a three-dimensional projection of the samples onto the three principal components was made. For the theory and use of these tests, see Sokal and Sneath (1963), Schnell (1970), Atchley (1970), Genoways (1973), and Sneath and Sokal (1973).

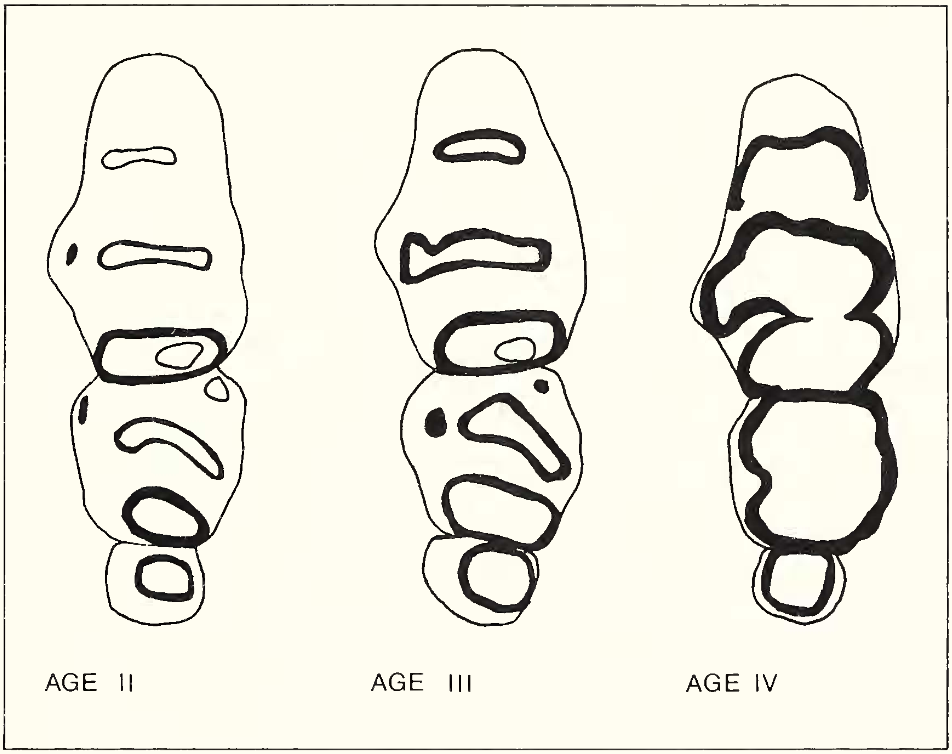

Fig. 1.—Diagrammatic representations (drawn from camera lucida) of left maxillary toothrows of *Steatomys cuppedius* illustrating wear pattern for age categories II, III, and IV individuals. Age category I, not shown, is the same as shown for category II, except that M^3 is not fully erupted.

NONGEOGRAPHIC VARIATION

The kinds of nongeographic variation considered in the study include secondary sexual, age, and individual variation. Individuals were first sorted by sex and age and tested for nongeographic variation with samples maintained in separate age and sex categories (Straney, 1978). This method should keep separate the effect of age and sex upon nongeographic variation. Then, in the absence of significant secondary sexual variation in each age category, the sexes were combined in the geographic samples used for the analysis of age variation.

Secondary Sexual Variation

Specimens from selected populations of *Steatomys cuppedius* and *S. caurinus* were assigned to one of four age categories (see section on Age Variation for details of ageing method and criteria). *Steatomys cuppedius* males and females of age categories II and III from Panisau, Nigeria, and age category II from Senegal were tested for significant differences in size. Similar tests between various ages of samples of male and female *S. caurinus* from Pirisi, Ghana (age II and III); Gudi, Nigeria (age III); and Cella, Upper Volta (age II) were performed. These samples were tested as only those populations and age categories from which sufficient individuals of both sexes were available could be analyzed.

The results of these tests on age category II individuals of *S. cuppedius* from Panisau, Nigeria, and of *S. caurinus* from Pirisi, Ghana, are shown in Table 1, whereas the results for age category III of the same geographic samples are listed in Table 2. The data for the other comparisons given above are not presented but are on file in the Section of Mammals, Carnegie Museum of Natural History.

Steatomys caurinus.—No significant differences in measurements between 16 males and 20 females from Gudi, Nigeria (age III), 13 males and 14 females from Cella, Upper Volta (age II), and 14 males and nine females from Pirisi, Ghana (age II) were found. The results of the latter comparison are

Table 1.—*Secondary sexual variation in external and cranial measurements of age category II specimens of* Steatomys caurinus *from Pirisi, Ghana, and* S. cuppedius *from Panisau, Nigeria. Means for males and females that are significantly different at the 5% level are marked with an asterisk.*

Measurements and sex	N	Mean ± 2 SE	Range	CV
Steatomys caurinus				
Total length				
Male	11	139.4 ± 5.38	130–156	6.4
Female	9	133.4 ± 4.10	128–147	4.6
Length of tail				
Male	11	38.8 ± 1.54	34–41	6.6
Female	9	39.4 ± 2.16	35–46	8.2
Length of hindfoot				
Male	11	19.0 ± 0.38	18–20	3.3
Female	9	18.4 ± 0.59	17–20	4.8
Length of ear				
Male	11	16.3 ± 0.55	15–18	5.6
Female	9	15.8 ± 0.44	15–17	4.2
Weight				
Male	11	34.4 ± 7.40	19–60	35.7
Female	9	32.2 ± 4.73	22–47	22.0
Greatest length of skull				
Male	8	24.4 ± 0.54	23.4–25.7	3.1
Female	4	23.7 ± 0.46	23.2–24.2	1.9
Condylobasal length				
Male	7	23.2 ± 0.46	22.5–24.3	2.6
Female	6	22.7 ± 0.53	22.0–23.4	2.8
Zygomatic breadth				
Male	8	12.1 ± 0.28	11.4–12.6	3.3
Female	3	11.8 ± 0.35	11.5–12.1	2.5
Interorbital breadth				
Male	11	3.8 ± 0.09	3.7–4.1	4.1
Female	8	3.8 ± 0.14	3.6–4.1	5.1
Rostral breadth				
Male	11	4.5 ± 0.10	4.3–4.8	3.5
Female	9	4.3 ± 0.15	4.0–4.7	5.1
Oblique length of bulla				
Male	7	5.4 ± 0.11	5.1–5.5	2.8
Female	4	5.3 ± 0.19	5.1–5.5	3.6
Greatest length of bulla				
Male	7	8.0 ± 0.18	7.8–8.4	3.0
Female	3	8.2 ± 0.07	8.1–8.2	0.7
Length of maxillary toothrow				
Male	10	4.1 ± 0.13	3.8–4.4	5.0
Female	9	3.9 ± 0.09	3.6–4.1	3.6
Breadth across upper molars				
Male	11	5.6 ± 0.10	5.4–5.9	2.9
Female	9	5.5 ± 0.14	5.3–5.9	3.7
Length of anterior palatal foramen				
Male	11	4.7 ± 0.14	4.2–5.2	4.9
Female	9	4.6 ± 0.19	3.9–4.9	6.2
Length of posterior palatal foramen				
Male	10	0.4 ± 0.07	0.2–0.5	24.6
Female	9	0.4 ± 0.06	0.3–0.6	20.0
Length of diastema				
Male	11	6.5 ± 0.19	5.9–7.0	4.8
Female	8	6.2 ± 0.20	5.7–6.5	4.6
Height of skull				
Male	6	8.7 ± 0.23	8.4–9.1	3.3
Female	5	8.5 ± 0.24	8.3–9.0	3.2
Length of mandibular toothrow				
Male	11	3.5 ± 0.12	3.2–3.9	5.9
Female	9	3.4 ± 0.14	3.0–3.7	6.2
Steatomys cuppedius				
Total length				
Male	24	109.7 ± 3.5	97–129	3.5
Female	9	106.3 ± 4.3	94–112	4.3
Length of tail				
Male	24	42.8 ± 1.4	38–50	8.0
Female	8	42.1 ± 1.9	37–45	6.3
Length of hindfoot				
Male	24	15.9 ± 0.18	15–17	2.8
Female	9	15.6 ± 0.48	14–16	4.7
Length of ear				
Male	24	12.7 ± 0.22	12–14	4.3
Female	9	12.4 ± 0.35	12–13	4.2
Weight				
Male	24	9.4 ± 0.90	6–14	23.4
Female	9	8.7 ± 1.25	5–10	21.6
Greatest length of skull				
Male	20	19.7 ± 0.30	18.4–21.4	3.5
Female	8	19.2 ± 0.63	17.5–20.3	4.6
Condylobasal length				
Male	21	18.5 ± 0.30	17.5–20.0	3.8
Female	8	18.0 ± 0.58	16.4–18.9	4.6
Zygomatic breadth				
Male	23	10.8 ± 0.14	10.3–11.5	3.0
Female	9	10.8 ± 0.26	10.2–11.5	3.5
Interorbital breadth				
Male	24	3.6 ± 0.05	3.3–3.9	3.6
Female	9	3.7 ± 0.08	3.5–3.9	3.4
Rostral breadth				
Male	24	3.7 ± 0.08	3.3–4.1	5.6
Female	9	3.7 ± 0.12	3.5–3.9	4.6

Table 1.—*Continued*

Measurements and sex	N	Mean ± 2 SE	Range	CV
Oblique length of bulla				
Male	17	4.5 ± 0.09	4.2–4.9	4.0
Female	6	4.5 ± 0.25	4.0–4.9	6.9
Greatest length of bulla				
Male	15	6.8 ± 0.13	6.4–7.3	3.8
Female	6	6.7 ± 0.26	6.2–7.1	4.8
Length of maxillary toothrow				
Male	23	3.6 ± 0.07	3.3–4.0	4.8
Female	9	3.7 ± 0.12	3.4–3.9	5.1
Breadth across upper molars				
Male	24	4.9 ± 0.09	4.4–5.6	4.6
Female	9	4.9 ± 0.13	4.6–5.2	4.0
Length of anterior palatal foramen				
Male	23	3.7 ± 0.09	3.1–4.0	5.6
Female	9	3.6 ± 0.19	3.2–4.2	8.2
Length of posterior palatal foramen*				
Male	22	0.4 ± 0.03	0.3–0.5	18.3
Female	9	0.5 ± 0.05	0.4–0.6	15.9
Length of diastema*				
Male	24	4.6 ± 0.10	4.1–5.0	5.3
Female	9	4.3 ± 0.05	4.2–4.4	1.8
Height of skull				
Male	18	7.6 ± 0.10	7.2–7.9	2.8
Female	6	7.5 ± 0.16	7.2–7.7	2.6
Length of mandibular toothrow				
Male	22	3.1 ± 0.06	2.9–3.4	4.3
Female	9	3.1 ± 0.13	2.7–3.3	6.4

given in Table 1. In age category III, individuals from Pirisi, Ghana, females were found to be significantly larger than males only in rostral breadth (Table 2).

Steatomys cuppedius.—No significant differences in size between 17 males and nine females of age category II from Senegal were found. However, in age category II from Panisau, Nigeria, the length of the posterior palatal foramen was larger in females, whereas the length of diastema was larger in males (Table 1). In the population from Panisau, Nigeria, males and females of age category III were found not to differ significantly in size (Table 2).

Conclusions.—No significant differences in size between males and females are obvious. From the comparisons of sexes of two age categories from five geographic samples, only two cranial measure-

Table 2.—*Secondary sexual variation in external and cranial measurements of age category III specimens of* Steatomys caurinus *from Pirisi, Ghana, and* S. cuppedius *from Panisau, Nigeria. Significance levels are the same as for Table 1.*

Measurements and sex	N	Mean ± 2 SE	Range	CV
Steatomys caurinus				
Total length				
Male	14	158.2 ± 4.59	137–169	5.4
Female	7	157.6 ± 5.70	145–165	4.8
Length of tail				
Male	14	43.1 ± 3.15	36–59	13.7
Female	7	41.4 ± 2.65	36–46	8.5
Length of hindfoot				
Male	14	19.7 ± 0.39	18–21	3.7
Female	7	19.6 ± 0.40	19–20	2.7
Length of ear				
Male	14	17.2 ± 0.43	16–18	4.7
Female	7	17.1 ± 0.68	16–18	5.2
Weight				
Male	14	54.4 ± 5.08	37–68	17.5
Female	7	53.3 ± 8.31	34–66	20.6
Greatest length of skull				
Male	12	26.4 ± 0.47	24.9–27.8	3.1
Female	5	26.3 ± 0.78	25.6–27.6	3.3
Condylobasal length				
Male	12	25.3 ± 0.53	23.5–26.6	3.6
Female	5	25.3 ± 0.63	24.7–26.4	2.8
Zygomatic breadth				
Male	12	12.9 ± 0.22	12.2–13.4	3.0
Female	4	13.0 ± 0.43	12.7–13.6	3.3
Interorbital breadth				
Male	14	3.9 ± 0.10	3.6–4.2	4.7
Female	6	3.9 ± 0.17	3.6–4.2	5.2
Rostral breadth*				
Male	14	4.8 ± 0.13	4.4–5.1	5.2
Female	7	5.0 ± 0.17	4.7–5.3	4.4
Oblique length of bulla				
Male	13	5.8 ± 0.12	5.5–6.3	3.7
Female	4	6.0 ± 0.17	5.8–6.2	2.9
Greatest length of bulla				
Male	10	8.8 ± 0.21	8.4–9.2	3.8
Female	5	8.8 ± 0.17	8.5–9.0	2.2
Length of maxillary toothrow				
Male	14	4.0 ± 0.09	3.7–4.3	4.1
Female	7	4.1 ± 0.17	3.8–4.4	5.6
Breadth across upper molars				
Male	14	5.9 ± 0.11	5.6–6.2	3.5
Female	7	6.1 ± 0.17	5.8–6.4	3.8

Table 2.—*Continued*

Measurements and sex	N	Mean ± 2 SE	Range	CV
Length of anterior palatal foramen				
Male	14	5.0 ± 0.11	4.7–5.4	4.0
Female	7	5.2 ± 0.24	4.7–5.6	6.2
Length of posterior palatal foramen				
Male	14	0.5 ± 0.09	0.3–0.8	31.0
Female	7	0.6 ± 0.16	0.3–1.0	38.6
Length of diastema				
Male	14	7.2 ± 0.19	6.5–7.8	4.9
Female	7	7.3 ± 0.22	7.0–7.7	4.0
Height of skull				
Male	10	9.2 ± 0.25	8.4–9.7	4.3
Female	4	9.3 ± 0.25	9.0–9.5	2.6
Length of mandibular toothrow				
Male	13	3.5 ± 0.13	3.1–3.9	6.8
Female	7	3.4 ± 0.13	3.2–3.7	5.0
Steatomys cuppedius				
Total length				
Male	8	118.3 ± 5.82	107–133	7.0
Female	8	117.9 ± 4.86	105–125	5.8
Length of tail				
Male	8	44.0 ± 2.98	39–52	9.6
Female	8	43.3 ± 2.67	37–48	8.7
Length of hindfoot				
Male	8	16.0 ± 0.38	15–17	3.3
Female	8	16.0 ± 0.53	15–17	4.7
Length of ear				
Male	8	13.5 ± 0.38	13–14	4.0
Female	8	12.9 ± 0.59	12–14	6.5
Weight				
Male	8	12.1 ± 2.08	8–17	24.3
Female	8	13.3 ± 1.55	10–17	16.5
Greatest length of skull				
Male	8	20.5 ± 0.47	19.6–21.4	3.2
Female	8	20.8 ± 0.41	20.1–21.6	2.8
Condylobasal length				
Male	8	19.4 ± 0.51	18.1–20.2	3.7
Female	8	19.6 ± 0.37	19.1–20.6	2.7
Zygomatic breadth				
Male	8	11.1 ± 0.26	10.5–11.5	3.4
Female	8	11.3 ± 0.25	10.7–11.8	3.2
Interorbital breadth				
Male	8	3.6 ± 0.13	3.4–4.0	5.1
Female	8	3.7 ± 0.07	3.6–3.8	2.7
Rostral breadth				
Male	8	3.9 ± 0.14	3.6–4.1	4.9
Female	8	3.9 ± 0.14	3.7–4.3	5.0

Table 2.—*Continued*

Measurements and sex	N	Mean ± 2 SE	Range	CV
Oblique length of bulla				
Male	6	4.7 ± 0.08	4.5–4.8	2.2
Female	8	4.7 ± 0.08	4.5–4.8	2.5
Greatest length of bulla				
Male	6	7.0 ± 0.12	6.7–7.1	2.2
Female	7	7.1 ± 0.26	6.4–7.4	4.8
Length of maxillary toothrow				
Male	8	3.6 ± 0.10	3.4–3.9	4.1
Female	8	3.7 ± 0.13	3.5–4.0	4.9
Breadth across upper molars				
Male	8	5.1 ± 0.16	4.6–5.3	4.4
Female	8	5.1 ± 0.12	4.9–5.4	3.4
Length of anterior palatal foramen				
Male	8	4.0 ± 0.24	3.4–4.4	8.5
Female	8	3.9 ± 0.15	3.5–4.2	5.4
Length of posterior palatal foramen				
Male	7	0.4 ± 0.07	0.3–0.5	21.7
Female	8	0.4 ± 0.05	0.3–0.5	18.9
Length of diastema				
Male	8	5.0 ± 0.14	4.7–5.2	4.0
Female	8	4.9 ± 0.12	4.6–5.1	3.4
Height of skull				
Male	6	7.8 ± 0.16	7.6–8.1	2.5
Female	8	7.8 ± 0.19	7.5–8.2	3.4
Length of mandibular toothrow				
Male	8	3.1 ± 0.11	2.7–3.2	5.2
Female	8	3.1 ± 0.10	2.9–3.3	4.4

ments were found to be significantly different—in individuals of *S. cuppedius* from Panisau, Nigeria. Therefore, in all subsequent analyses the sexes were pooled.

Age Variation

Age categories used in this study are shown in Fig. 1; these categories are usually referred to as follows: Age I, juveniles; Age II, subadults; Age III, young adults; Age IV, adults. Age I is not illustrated in Fig. 1; M^3 in this age category has not erupted fully. These categories are arbitrary, based on dental wear, and do not reflect reproductive age. *Steatomys cuppedius* populations tested for age variation are the Senegal population, which had sufficient sample sizes in categories I, II, and III, and the Panisau, Nigeria, sample, which had adequate numbers in categories I, III, and IV. Those

Table 3.—*Variation with age in external and cranial measurements of* Steatomys caurinus *from Yama, Ivory Coast, and* S. cuppedius *from Panisau, Nigeria. Age classes are listed in decreasing order from the largest mean. Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 5% level. Groups of means of nonsignificant differences are labelled "ns."*

Measurements and age classes	N	Mean ± 2 SE	Range	CV	SS-STP		
Steatomys caurinus							
Total length							
IV	10	166.8 ± 8.00	155–200	7.5	│		
III	13	147.8 ± 6.54	134–169	8.0		│	
II	14	135.3 ± 2.64	121–156	6.5			│
Length of tail							
IV	10	52.7 ± 3.94	45–64	11.8	│		
III	13	45.7 ± 3.16	38–58	12.5		│	
II	44	44.1 ± 1.55	35–55	11.7		│	
Length of hindfoot							
IV	10	19.0 ± 0.73	17–21	6.1			
III	13	18.8 ± 0.51	18–20	4.9	ns		
II	44	18.5 ± 0.25	17–20	4.4			
Length of ear							
IV	10	18.1 ± 0.55	17–20	4.8	│		
III	13	17.7 ± 0.53	16–20	5.4	│		
II	44	16.7 ± 0.27	15–19	5.3		│	
Weight							
IV	10	41.8 ± 4.66	35–58	17.6	│		
III	13	32.0 ± 6.38	22–54	35.9		│	
II	14	22.7 ± 1.86	12–38	27.2			│
Greatest length of skull							
IV	0						
III	4	25.4 ± 1.14	24.3–26.5	4.5	│		
II	11	23.7 ± 0.35	22.7–24.6	2.4		│	
Condylobasal length							
IV	5	25.8 ± 0.79	24.6–26.7	3.4	│		
III	9	23.9 ± 0.63	22.8–25.3	4.0		│	
II	29	22.7 ± 0.33	20.8–23.9	3.9			│
Zygomatic breadth							
IV	4	13.2 ± 0.24	12.9–13.4	1.8	│		
III	7	12.3 ± 0.53	11.3–13.0	5.7		│	
II	23	11.7 ± 0.20	10.7–12.5	4.1		│	
Interorbital breadth							
IV	9	4.1 ± 0.07	3.9–4.2	2.5	│		
III	12	3.9 ± 0.07	3.6–4.1	3.3	│	│	
II	38	3.8 ± 0.05	3.4–4.1	4.4		│	
Rostral breadth							
IV	9	5.1 ± 0.15	4.9–5.5	4.3	│		
III	13	4.4 ± 0.11	4.1–4.7	4.5		│	
II	39	4.2 ± 0.06	3.9–4.6	4.3			│
Oblique length of bulla							
IV	7	5.8 ± 0.24	5.3–6.1	5.6	│		
III	10	5.4 ± 0.15	4.9–5.7	4.3		│	
II	34	5.3 ± 0.08	4.8–5.7	4.2		│	
Greatest length of bulla							
IV	6	9.0 ± 0.33	8.6–9.5	4.5	│		
III	8	8.4 ± 0.18	8.0–8.8	3.1		│	
II	31	8.2 ± 0.09	7.7–8.7	3.2		│	
Length of maxillary toothrow							
IV	10	4.1 ± 0.14	3.7–4.4	5.5			
III	13	4.1 ± 0.10	3.8–4.4	4.3	ns		
II	42	4.0 ± 0.05	3.6–4.4	4.0			
Breadth across upper molars							
IV	8	6.1 ± 0.16	5.8–6.5	3.8	│		
III	12	5.7 ± 0.10	5.4–6.1	3.1		│	
II	37	5.5 ± 0.07	5.1–6.1	3.6		│	
Length of anterior palatal foramen							
IV	9	5.6 ± 0.13	5.3–5.9	3.4	│		
III	12	4.9 ± 0.19	4.4–5.4	6.7		│	
II	37	4.6 ± 0.11	4.2–5.9	7.1		│	
Length of posterior palatal foramen							
IV	7	0.5 ± 0.10	0.3–0.7	26.2			
III	11	0.5 ± 0.07	0.3–0.7	23.1	ns		
II	32	0.5 ± 0.04	0.3–0.7	24.3			
Length of diastema							
IV	9	7.2 ± 0.24	6.8–8.0	5.0	│		
III	13	6.3 ± 0.30	5.6–7.4	8.7		│	
II	40	6.0 ± 0.10	5.2–6.6	5.4			│
Height of skull							
IV	4	9.6 ± 0.15	9.5–9.8	1.6	│		
III	9	9.0 ± 0.23	8.6–9.7	3.9		│	
II	26	8.7 ± 0.10	8.3–9.1	3.0			│
Length of mandibular toothrow							
IV	10	3.6 ± 0.18	3.1–4.1	8.1			
III	13	3.5 ± 0.08	3.2–3.7	4.3	ns		
II	43	3.5 ± 0.05	3.2–3.9	4.9			
Steatomys cuppedius							
Total length							
IV	6	132.7 ± 7.04	120–143	6.5	│		
III	16	118.1 ± 3.66	105–133	6.2		│	
II	33	108.8 ± 2.85	94–129	7.5			│
Length of tail							
IV	6	48.7 ± 2.29	46–54	5.8	│		
III	16	43.6 ± 1.94	37–52	8.9		│	
II	32	42.6 ± 1.14	37–50	7.5		│	
Length of hindfoot							
IV	6	16.0 ± 0.52	15–17	4.0			
III	16	16.0 ± 0.32	15–17	4.0	ns		
II	33	15.8 ± 0.19	14–17	3.5			

Table 3.—*Continued.*

Measurements and age classes	N	Mean ± 2 SE	Range	CV	SS-STP
Length of ear					
IV	6	13.7 ± 0.42	13–14	3.8	│
III	16	13.2 ± 0.38	12–14	5.7	│
II	33	12.6 ± 0.19	12–14	4.3	│
Weight					
IV	6	16.2 ± 2.75	13–22	20.9	│
III	16	12.7 ± 1.29	8–17	20.3	│
II	33	9.2 ± 0.74	5–14	23.0	│
Greatest length of skull					
IV	5	22.4 ± 0.88	21.3–23.9	4.4	│
III	16	20.7 ± 0.31	19.6–21.6	3.0	│
II	28	19.5 ± 0.29	17.5–21.4	3.9	│
Condylobasal length					
IV	6	21.0 ± 0.76	20.1–22.5	4.5	│
III	16	19.5 ± 0.31	18.1–20.6	3.2	│
II	29	18.3 ± 0.28	16.4–20.0	4.1	│
Zygomatic breadth					
IV	6	11.8 ± 0.38	11.2–12.4	4.0	│
III	16	11.2 ± 0.19	10.5–11.8	3.4	│
II	32	10.8 ± 0.12	10.2–11.5	3.1	│
Interorbital breadth					
IV	6	3.9 ± 0.16	3.6–4.1	5.0	│
III	16	3.7 ± 0.07	3.4–4.0	4.0	│
II	33	3.6 ± 0.05	3.3–3.9	3.6	│
Rostral breadth					
IV	6	4.2 ± 0.24	3.9–4.7	6.9	│
III	16	3.9 ± 0.09	3.6–4.3	4.8	│
II	33	3.7 ± 0.07	3.3–4.1	5.3	│
Oblique length of bulla					
IV	5	4.8 ± 0.23	4.4–5.0	5.3	│
III	14	4.7 ± 0.06	4.5–4.8	2.3	│
II	23	4.5 ± 0.09	4.0–4.9	4.7	│
Greatest length of bulla					
IV	5	7.4 ± 0.19	7.1–7.7	2.9	│
III	13	7.1 ± 0.15	6.4–7.4	4.0	│
II	21	6.8 ± 0.12	6.2–7.3	4.0	│
Length of maxillary toothrow					
IV	6	3.8 ± 0.12	3.6–4.0	3.9	
III	16	3.7 ± 0.09	3.4–4.0	4.7	ns
II	32	3.6 ± 0.06	3.3–4.0	4.9	
Breadth across upper molars					
IV	6	5.3 ± 0.19	5.1–5.7	4.4	│
III	16	5.1 ± 0.10	4.6–5.4	3.8	│
II	33	4.9 ± 0.07	4.4–5.6	4.3	│
Length of anterior palatal foramen					
IV	6	4.2 ± 0.18	4.0–4.6	5.3	│
III	16	4.0 ± 0.14	3.4–4.4	6.9	│
II	32	3.7 ± 0.08	3.1–4.2	6.5	│

Table 3.—*Continued.*

Measurements and age classes	N	Mean ± 2 SE	Range	CV	SS-STP
Length of posterior palatal foramen					
IV	6	0.4 ± 0.08	0.3–0.5	20.4	
III	15	0.4 ± 0.04	0.3–0.5	20.3	ns
II	31	0.4 ± 0.03	0.3–0.6	18.5	
Length of diastema					
IV	6	5.3 ± 0.35	4.8–5.9	8.0	│
III	16	5.0 ± 0.09	4.6–5.2	3.8	│
II	33	4.5 ± 0.08	4.1–5.0	5.4	│
Height of skull					
IV	6	8.2 ± 0.18	8.0–8.5	2.7	│
III	14	7.8 ± 0.12	7.5–8.2	2.9	│
II	24	7.6 ± 0.08	7.2–7.9	2.7	│
Length of mandibular toothrow					
IV	6	3.4 ± 0.12	3.2–3.6	4.5	│
III	16	3.1 ± 0.07	2.7–3.3	4.7	│
II	31	3.1 ± 0.05	2.7–3.4	4.9	│

populations of *S. caurinus* tested were from Yama, Ivory Coast, with sufficient individuals of categories II, III, and IV; Pirisi, Ghana (II and III); Gudi, Nigeria (II and III); and Cella, Upper Volta (II and III). For each of the 19 external and cranial measurements, samples of combined sexes were tested to determine if the differences between the means of the age categories were significantly different ($P \leq 0.05$). If found to be significantly different, the Sum of Squares Simultaneous Test Procedure was used to find maximally nonsignificant subsets. The results of these tests in *S. cuppedius* from Panisau, Nigeria (age II, III, IV), and *S. caurinus* from Yama, Ivory Coast (age II, III, IV), are presented (Table 3).

Steatomys caurinus.—In the population from Yama, Ivory Coast, nonoverlapping subsets among age categories II, III, and IV were found in six (total length, weight, condylobasal length, rostral breadth, diastemal length, and height of skull) of 19 measurements; no greatest length of skull measurements are available for age category IV in this sample. Little or no variation in age exists in the following measurements: length of hindfoot; interorbital breadth; lengths of maxillary toothrow; posterior palatal foramen; mandibular toothrow. A similar trend was found in the other populations of *S. caurinus* tested but is not presented in tabular form.

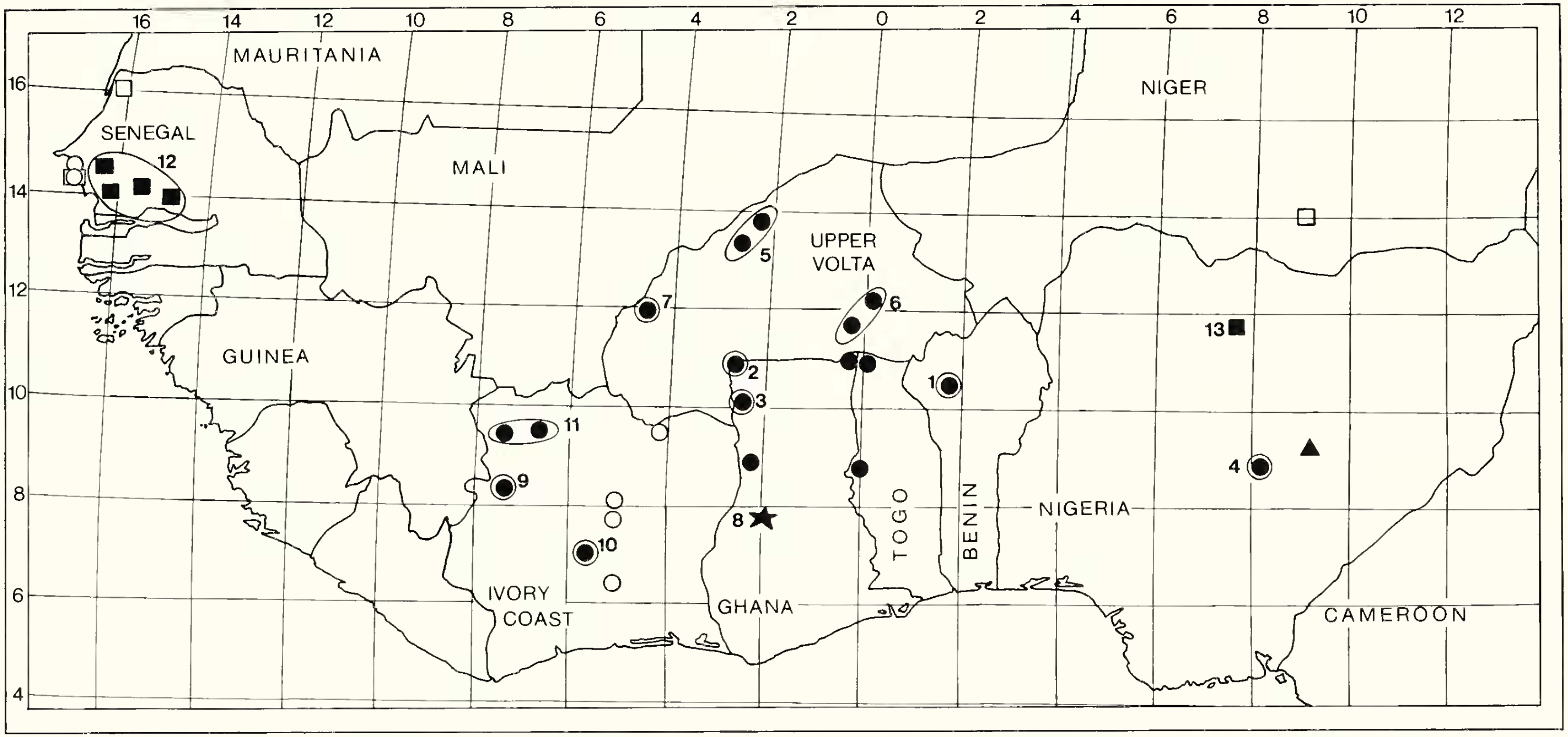

Fig. 2.—Distribution of West African taxa of *Steatomys* showing type localities for each taxon, literature records and specimens examined. OTUs are designated, with inclusive individual localities, by numbers. See text for list of localities included in each OTU. Solid symbols represent localities of specimens examined; open symbols represent localities of literature records. Solid star represents type locality of *S. jacksoni*. Solid triangle represents type locality of *S. caurinus;* the remaining localities of this species are represented by solid or open circles. Solid square indicating OTU 13 represents the type locality of *S. cuppedius*; the remaining localities of this species are represented by solid or open squares. Both *S. caurinus* and *S. cuppedius* are reported from M'Bour, Senegal.

Steatomys cuppedius.—Three nonoverlapping subsets among age categories II, III, and IV in nine (total length, weight, greatest length of skull, condylobasal length, zygomatic breadth, rostral breadth, greatest length of bulla, length of diastema, and height of skull) of 19 measurements were found in the population from Panisau, Nigeria (Table 3). Three characters (lengths of hindfoot, maxillary toothrow, and anterior palatal foramen) showed no significant differences among the different age categories tested. In comparing measurements from the different age categories (I, II, and III) in the population from Senegal, a similar trend emerges, although it is not presented in tabular form.

Conclusions.—From these results, it is apparent that none of the age categories can be pooled in either species for a study of geographic variation. It would be ideal if age IV (adult) specimens could be used for a study of geographic variation in these species. However, due to a lack of sufficient samples of age IV specimens, only specimens belonging to age category III were used.

Individual Variation

The majority of measurements examined revealed a relatively low degree of individual variation as expressed by the coefficient of variation. External measurements were generally more variable than the cranial measurements (Tables 1, 2, 3). This was, however, not as pronounced in *Steatomys cuppedius* as in *Steatomys caurinus*. Of external measurements, weight showed the most variation, with coefficients of variation above 20. Cranial measurements in both species usually had coefficients of variation of less than 5, except in length of posterior palatal foramen where these values usually were above 15.

Conclusions.—Due to the tendency of the external measurements, especially weight, to show relatively higher individual variation expressed as coefficients of variation than did the cranial measurements, all external measurements were excluded from the multivariate analyses of geographic variation. Of the cranial measurements, length of posterior palatal foramen was excluded from this analysis due to its high level of individual variation.

RELATIONSHIPS OF SPECIES

All individuals from West Africa of age category III, and a few specimens that were borderline between category III and IV in age, were grouped into 13 geographic samples. These geographic samples (OTUs) are as follows (see also Fig. 2): 1) Kouande, Benin; 2) Bangwon, Ghana; 3) Pirisi, Ghana; 4) Gudi, Nigeria; 5) Dio and Barga, Upper Volta; 6) Cella and Nayoure, Upper Volta; 7) Fo, Upper Volta; 8) Wenchi, Ghana; 9) Tyenko, Ivory Coast; 10) Diali, Ivory Coast; 11) Sienso and Yama, Ivory Coast; 12) Diourbel, Kaffrine, Kaolack and Kougheul, Senegal; and 13) Panisau, Nigeria.

Steatomys caurinus was described by Thomas (1912) as being generally brownish fawn, but with a darker mid-dorsal area and more distinct color along the sides of the belly. Rosevear (1969) summarized the color of *S. caurinus* as being "medium warm reddish brown" (the tips of the hair were warm brown and the bases were dark gray). According to the description by Hayman (1936), the dorsal pelage of *S. jacksoni* is plumbeous drab in color, with the flanks slightly paler, whereas Rosevear (1969) describes this species as being dark brownish-gray in color of pelage. A large number of the specimens examined in the present study have skins soiled by residual fats and oils, making an accurate definition of an already variable character, color of pelage, difficult. The dorsal pelage color of *S. cuppedius* was described originally by Thomas and Hinton (1920) as being pale drab with pale sides, and more recently by Rosevear (1969) as being pale, slightly sandy gray. Specimens of this species generally did not have soiled skins such as was found for *S. caurinus*.

Hayman (1936) stated in the original description of *S. jacksoni* that the braincase of the holotype was not sharply truncated as in other species of the genus he had examined, and that the interparietal was lengthened from front to back and noticeably widened anteroposteriorly in the middle part. We have found in the present study that the older animals, such as age category IV individuals, exhibit relatively less truncated skulls than do the younger animals. Hayman (1936) gave a length of 4.5 mm for the interparietal of *S. jacksoni* as compared to 2.5 mm in *S. caurinus*. The length of the interparietal bone of all specimens examined in the present study, with the exception of the holotype of *S. jack-*

Table 4.—*Geographic variation in external and cranial measurements of age category III individuals among 10 geographic samples (OTUs) of* Steatomys caurinus *and two geographic samples of* S. cuppedius. *Results of ANOVA analysis indicating significance at the 5% level for* S. cuppedius *are indicated by an asterisk next to the character heading. See Fig. 2 and text for key to localities included in each OTU.*

Sample	N	Mean ± 2 SE	Range	CV
		Steatomys caurinus		
		Total length		
1	1	167.0		
2	2	129.0	121–137	
3	21	158.0 ± 3.52	137–169	5.1
4	36	159.2 ± 3.93	126–178	7.4
5	2	142.5	142–143	
6	18	161.2 ± 5.82	136–178	7.7
7	1	154.0		
9	5	164.4 ± 9.11	149–173	6.2
10	3	168.7 ± 27.1	142–186	13.9
11	15	148.6 ± 6.48	134–169	8.4
		Length of tail		
1	1	48.0		
2	2	37.0	35–39	
3	21	42.5 ± 2.26	36–59	12.2
4	36	45.9 ± 0.21	37–52	7.9
5	2	40.0	38–42	
6	18	45.8 ± 2.09	40–53	9.7
7	1	51.0		
9	5	55.4 ± 3.2	50–59	6.5
10	3	59.0 ± 12.5	47–68	18.3
11	15	46.6 ± 3.33	38–60	13.8
		Length of hindfoot		
1	1	18.0		
2	2	17.5	17–18	
3	21	19.7 ± 0.29	18–21	3.3
4	36	19.7 ± 0.21	18–21	3.2
5	2	19.0	19	
6	18	18.8 ± 0.50	17–21	5.6
7	1	18.0		
9	5	19.0 ± 1.10	17–20	6.4
10	3	19.0 ± 1.15	18–20	5.3
11	15	18.7 ± 0.46	18–20	4.7
		Length of ear		
1	1	16.0		
2	2	15.5	15–16	
3	21	17.2 ± 0.36	16–18	4.7
4	36	17.6 ± 0.36	15–20	6.1
5	2	15.0	15	
6	18	17.1 ± 0.57	14–19	7.1
7	1	18.0		
9	5	17.4 ± 0.49	17–18	3.4
10	3	18.0 ± 2.0	16–19	9.6
11	15	17.7 ± 0.54	16–20	5.9
		Weight		
1	1	28.0		
2	2	31.5	26–37	
3	21	54.0 ± 4.26	34–68	18.1
4	35	48.2 ± 3.56	25–68	21.9
5	2	30.5	30–31	
6	18	48.4 ± 5.35	23–70	23.4
7	1	17.0		
9	5	39.6 ± 7.71	32–53	21.8
10	3	51.3 ± 24.0	29–70	40.4
11	15	31.7 ± 5.59	22–54	34.2
		Greatest length of skull		
1	1	—		
2	2	—		
3	17	26.4 ± 0.39	24.9–27.8	3.1
4	32	26.6 ± 0.38	24.2–28.4	4.0
5	1	23.7		
6	9	26.6 ± 0.72	24.3–28.0	4.1
7	1	25.5		
9	2	27.6 ± 1.00	27.1–28.1	2.6
10	3	—		
11	5	25.2 ± 1.03	24.1–26.5	4.6
		Condylobasal length		
1	1	—		
2	2	—		
3	17	25.3 ± 0.41	23.4–26.6	3.3
4	26	25.3 ± 0.37	23.1–27.0	3.7
5	2	23.0	22.6–23.4	
6	10	25.3 ± 0.87	22.8–27.0	5.5
7	1	24.2		
9	5	25.6 ± 1.05	23.8–27.0	4.6
10	3	25.7 ± 2.60	23.2–27.5	8.8
11	11	23.9 ± 0.68	22.5–25.8	4.7
		Zygomatic breadth		
1	1	—		
2	2	—		
3	16	13.0 ± 0.19	12.2–13.6	3.0
4	22	13.1 ± 0.23	12.2–13.8	4.1
5	1	12.0		
6	12	12.8 ± 0.31	12.0–13.6	4.2
7	1	12.4		
9	5	13.1 ± 0.61	12.1–13.8	5.2
10	3	13.5 ± 0.98	12.5–14.1	6.3
11	9	12.3 ± 0.51	11.3–13.5	6.2
		Interorbital breadth		
1	1	—		
2	1	3.5		
3	20	3.9 ± 0.08	3.6–4.2	4.7
4	34	3.9 ± 0.06	3.5–4.3	4.1
5	2	3.9	3.9	
6	18	3.9 ± 0.06	3.7–4.1	3.1
7	1	3.9		
9	5	4.2 ± 0.19	3.8–4.3	5.0
10	3	4.0 ± 0.29	3.8–4.3	6.2
11	14	3.9 ± 0.09	3.6–4.3	4.4
		Rostral breadth		
1	1	—		
2	2	4.1	4.0–4.2	
3	21	4.8 ± 0.12	4.4–5.3	5.5

Table 4.—*Continued.*

Sample	N	Mean ± 2 SE	Range	CV
4	35	4.7 ± 0.11	3.9–5.3	6.9
5	2	4.4	4.0–4.7	
6	17	4.9 ± 0.13	4.5–5.4	5.5
7	1	4.6		
9	5	4.8 ± 0.24	4.4–5.1	5.6
10	3	4.9 ± 0.58	4.4–5.4	10.3
11	15	4.5 ± 0.12	4.1–4.9	5.1
Oblique length of bulla				
1	1	—		
2	1	5.2		
3	17	5.9 ± 0.10	5.5–6.3	3.5
4	31	5.8 ± 0.09	5.2–6.5	4.3
5	2	6.0	5.5–6.5	
6	10	5.9 ± 0.19	5.6–6.5	5.0
7	1	5.7		
9	5	5.7 ± 0.24	5.4–6.0	4.8
10	3	6.0 ± 0.18	5.8–6.1	2.5
11	12	5.4 ± 0.15	4.9–5.9	4.7
Greatest length of bulla				
1	1	—		
2	1	8.0		
3	15	8.8 ± 0.15	8.4–9.2	3.3
4	30	9.0 ± 0.13	8.0–9.7	3.8
5	2	8.2	8.0–8.3	
6	9	8.7 ± 0.21	8.2–9.3	3.6
7	1	8.5		
9	5	9.0 ± 0.55	8.1–9.6	6.8
10	3	9.0 ± 0.80	8.8–9.4	3.8
11	10	8.6 ± 0.28	8.0–9.6	5.1
Length of maxillary toothrow				
1	1	—		
2	2	3.9	3.9	
3	21	4.1 ± 0.08	3.7–4.4	4.6
4	36	4.2 ± 0.05	3.8–4.5	3.8
5	2	4.0	3.8–4.1	
6	17	4.3 ± 0.10	3.9–4.6	4.9
7	1	3.8		
9	5	4.2 ± 0.12	4.1–4.4	3.1
10	3	4.1 ± 0.29	3.8–4.3	6.1
11	15	4.1 ± 0.08	3.8–4.4	4.0
Breadth across upper molars				
1	1	—		
2	2	5.5	5.4–5.5	
3	21	5.9 ± 0.10	5.6–6.4	3.7
4	34	6.0 ± 0.10	5.0–6.5	4.8
5	2	5.8	5.7–5.8	
6	17	5.9 ± 0.17	5.1–6.4	5.9
7	1	6.0		
9	5	6.0 ± 0.19	5.7–6.2	3.6
10	3	6.0 ± 0.42	5.7–6.4	6.0
11	14	5.7 ± 0.13	5.4–6.3	4.2
Length of anterior palatal foramen				
1	1	—		
2	2	4.3	4.0–4.5	
3	21	5.1 ± 0.11	4.7–5.6	4.9

Table 4.—*Continued.*

Sample	N	Mean ± 2 SE	Range	CV
4	35	4.8 ± 0.08	4.4–5.2	4.6
5	2	4.3	4.3	
6	13	5.1 ± 0.21	4.5–5.5	7.4
7	1	5.0		
9	5	5.3 ± 0.42	4.6–5.9	8.9
10	3	5.2 ± 0.70	4.6–5.8	11.6
11	14	4.9 ± 0.17	4.4–5.4	6.5
Length of posterior palatal foramen				
1	1	—		
2	2	0.5	0.4–0.5	
3	21	0.5 ± 0.08	0.3–1.0	33.0
4	30	0.5 ± 0.04	0.3–0.7	24.2
5	2	0.5	0.5	
6	17	0.6 ± 0.06	0.4–0.8	17.4
7	1	0.4		
9	5	0.5 ± 0.07	0.4–0.6	16.1
10	3	0.6 ± 0.31	0.4–0.9	44.1
11	15	0.5 ± 0.07	0.3–0.7	23.4
Length of diastema				
1	1	—		
2	2	6.2	6.0–6.4	
3	21	7.2 ± 0.15	6.5–7.8	4.6
4	36	7.0 ± 0.14	6.0–7.6	5.9
5	2	6.6	6.3–6.8	
6	17	7.0 ± 0.21	6.3–7.7	6.2
7	1	6.8		
9	5	6.9 ± 0.34	6.7–7.6	5.5
10	3	7.2 ± 1.00	6.3–8.0	12.0
11	15	6.3 ± 0.28	5.8–7.4	5.6
Height of skull				
1	1	—		
2	2	—		
3	14	9.2 ± 0.19	8.4–9.7	3.8
4	32	9.2 ± 0.17	7.7–10.1	5.2
5	2	9.2	8.7–9.6	
6	11	9.3 ± 0.24	8.5–10.0	4.3
7	1	9.1		
9	5	9.6 ± 0.41	8.9–10.0	4.7
10	3	9.9 ± 0.77	9.2–10.5	6.7
11	11	9.0 ± 0.20	8.6–9.2	3.8
Length of mandibular toothrow				
1	1	—		
2	2	3.3	3.3	
3	20	3.5 ± 0.10	3.1–3.9	6.2
4	34	3.5 ± 0.06	3.1–3.9	5.4
5	2	3.2	3.2	
6	16	3.5 ± 0.07	3.3–3.8	4.2
7	1	3.2		
9	5	3.5 ± 0.12	3.3–3.6	3.9
10	3	3.5 ± 0.29	3.2–3.7	7.2
11	15	3.5 ± 0.08	3.2–3.7	4.2
Steatomys cuppedius				
Total length*				
12	5	125.6 ± 2.58	122–130	2.3
13	16	118.1 ± 3.66	105–133	6.2

Table 4.—*Continued.*

Sample	N	Mean ± 2 SE	Range	CV
Length of tail				
12	5	44.8 ± 1.60	43–47	4.0
13	16	43.6 ± 1.94	37–52	8.9
Length of hindfoot				
12	5	15.8 ± 0.40	15–16	2.8
13	16	16.0 ± 0.32	15–17	4.0
Length of ear				
12	5	12.8 ± 0.40	12–13	3.5
13	16	13.2 ± 0.38	12–14	5.7
Weight*				
12	5	16.8 ± 5.31	7–23	35.3
13	16	12.7 ± 1.29	8–17	20.3
Greatest length of skull*				
12	2	22.0 ± 0.40	21.8–22.2	1.3
13	16	20.7 ± 0.31	19.6–21.6	3.0
Condylobasal length				
12	3	20.2 ± 0.35	19.9–20.5	1.5
13	16	19.5 ± 0.31	18.1–20.6	3.2
Zygomatic breadth				
12	2	11.6 ± 0.30	11.4–11.7	1.8
13	16	11.2 ± 0.19	10.5–11.8	3.4
Interorbital breadth				
12	5	3.6 ± 0.07	3.5–3.7	2.3
13	16	3.7 ± 0.07	3.4–4.0	4.0
Rostral breadth				
12	5	4.1 ± 0.14	3.9–4.3	3.9
13	16	3.9 ± 0.09	3.6–4.3	4.8
Oblique length of bulla*				
12	3	5.1 ± 0.12	5.0–5.2	2.0
13	14	4.7 ± 0.06	4.5–4.8	2.3
Greatest length of bulla				
12	2	7.5 ± 0.10	7.4–7.5	0.9
13	13	7.1 ± 0.15	6.4–7.4	4.0
Length of maxillary toothrow				
12	5	3.6 ± 0.16	3.4–3.9	5.0
13	16	3.7 ± 0.09	3.4–4.0	4.7
Breadth across upper molars				
12	4	5.1 ± 0.08	5.0–5.2	1.6
13	16	5.1 ± 0.10	4.6–5.4	3.8
Length of anterior palatal foramen				
12	3	4.2 ± 0.07	4.1–4.2	1.4
13	16	4.0 ± 0.14	3.4–4.4	6.9
Length of posterior palatal foramen				
12	4	0.4 ± 0.08	0.3–0.5	20.4
13	15	0.4 ± 0.04	0.3–0.5	20.3
Length of diastema				
12	4	5.1 ± 0.13	4.9–5.2	2.5
13	16	5.0 ± 0.09	4.6–5.2	3.8
Height of skull				
12	4	8.1 ± 0.47	7.4–8.4	5.9
13	14	7.8 ± 0.12	7.5–8.2	2.9
Length of mandibular toothrow				
12	4	3.2 ± 0.15	3.1–3.4	4.7
13	16	3.1 ± 0.07	2.7–3.3	4.7

soni, measured less than 4 mm. The interparietal bones varied in shape from nearly triangular to quadrangular. This variation in shape occurred among specimens within the same age category.

In his original description, Hayman (1936) concluded that *S. jacksoni* was not bigger than *S. caurinus*, but he compared only the external measurements of the two taxa. Thus the single most important character used by Hayman (1936) in describing *S. jacksoni* was the size and shape of the interparietal bone. When the holotype was examined, the interparietal bone did measure 4 mm in length and was clearly longer than any of the other specimens of *Steatomys* examined. Based on this diagnostic character, none of the specimens we examined could be assigned to *S. jacksoni.*

Univariate analysis.—Results of standard univariate statistical analysis for individuals of *Steatomys* from the 13 geographic samples are given in Tables 4 and 5. In age category III specimens (Table 4), there is no overlap in the range of measurements between geographic samples 12 and 13 (*S. cuppedius*) and those of the remainder of the West African geographic samples in four of the 19 characters analyzed (greatest length of skull, condylobasal length, greatest length of bulla, and length of diastema). Comparison of these same analyses for age category IV individuals (Table 5) reveals that 12 of 19 characters (total length, length of ear, weight, greatest length of skull, condylobasal length, zygomatic breadth, rostral breadth, oblique length of bulla, greatest length of bulla, width across upper molars, length of anterior palatal foramen, length of diastema, and height of skull) show no overlap between geographic samples 12 and 13 and the remaining geographic samples analyzed. *Steatomys cuppedius* is readily distinguishable from other West African fat mice in being markedly smaller in size, both externally and cranially, and much paler in color of pelage.

Table 5.—*Geographic variation in external and cranial measurements of age category IV individuals among six geographic samples (OTUs) of* Steatomys caurinus *and two geographic samples of* S. cuppedius. *See Fig. 2 and text for key to localities included in each OTU.*

Sample	N	Mean ± 2 SE	Range	CV
		Steatomys caurinus		
		Total length		
3	1	155		
4	2	166	162–170	
6	1	179		
9	1	188		
10	1	199		
11	10	166.8 ± 8.0	155–200	7.5
		Length of tail		
3	1	41		
4	2	43	41–45	
6	1	47		
9	1	65		
10	1	—		
11	10	52.7 ± 3.9	45–64	11.8
		Length of hindfoot		
3	1	18.0		
4	2	19.5	19–20	
6	1	18.0		
9	1	20		
10	1	21		
11	10	19.0 ± 0.73	17–21	6.1
		Length of ear		
3	1	17.0		
4	2	17.5	17–18	
6	1	18.0		
9	1	18.0		
10	1	18.0		
11	10	18.1 ± 0.55	17–20	4.8
		Weight		
3	1	56.0		
4	2	55.5	54–57	
6	1	70.0		
9	1	69.0		
10	1	69.0		
11	10	41.8 ± 4.66	35–58	17.6
		Greatest length of skull		
3	1	27.2		
4	1	29.3		
6	0			
9	1	28.5		
10	0			
11	0			
		Condylobasal length		
3	1	25.6		
4	1	28.0		
6	1	27.2		
9	1	27.1		
10	1	28.3		
11	5	25.8 ± 0.79	24.6–26.7	3.4
		Zygomatic breadth		
3	1	13.1		
4	1	15.1		
6	1	13.9		
9	1	14.2		
10	1	14.5		
11	4	13.2 ± 0.24	12.9–13.4	1.8
		Interorbital breadth		
3	1	4.2		
4	2	4.1	3.9–4.2	
6	1	4.1		
9	1	4.0		
10	1	4.2		
11	9	4.1 ± 0.07	3.9–4.2	2.5
		Rostral breadth		
3	1	4.8		
4	2	5.5	5.3–5.6	
6	1	5.5		
9	1	5.3		
10	1	5.4		
11	9	5.1 ± 0.15	4.9–5.5	4.3
		Oblique length of bulla		
3	1	5.8		
4	1	5.9		
6	0			
9	1	6.2		
10	1	6.1		
11	7	5.8 ± 0.33	8.6–9.5	4.5
		Greatest length of bulla		
3	1	9.0		
4	1	9.0		
6	0			
9	1	9.4		
10	1	9.9		
11	6	9.0 ± 0.33	8.6–9.5	4.5
		Length of maxillary toothrow		
3	1	3.9		
4	2	4.5	4.4–4.5	
6	1	4.4		
9	1	4.3		
10	1	3.9		
11	10	4.1 ± 0.14	3.7–4.4	5.5
		Breadth across upper molars		
3	1	6.0		
4	2	6.4	5.9–6.8	
6	1	6.2		
9	1	6.4		
10	1	6.1		
11	8	6.1 ± 0.16	5.8–6.5	3.8
		Length of anterior of anterior palatal foramen		
3	1	5.2		
4	1	5.1		

Table 5.—*Continued.*

Sample	N	Mean ± 2 SE	Range	CV
6	1	5.6		
9	1	5.2		
10	1	6.0		
11	9	5.6 ± 0.13	5.3–5.9	3.4
		Length of posterior palatal foramen		
3	1	0.7		
4	2	0.5	0.5	
6	1	0.6		
9	1	0.6		
10	1	0.5		
11	7	0.5 ± 0.10	0.3–0.7	26.2
		Length of diastema		
3	1	7.3		
4	2	7.5	6.9–8.0	
6	1	7.1		
9	1	7.4		
10	1	8.6		
11	9	7.2 ± 0.24	6.8–8.0	5.0
		Height of skull		
3	1	9.3		
4	1	10.6		
6	1	10.1		
9	1	10.5		
10	1	10.1		
11	4	9.6 ± 0.15	9.5–9.8	1.6
		Length of mandibular toothrow		
3	0			
4	2	3.6	3.5–3.6	
6	1	3.8		
9	1	3.7		
10	0			
11	10	3.6 ± 0.18	3.1–4.1	8.1
		Steatomys cuppedius		
		Total length		
12	2	125.0	124–125	
13	6	132.7 ± 7.04	120–143	6.5
		Length of tail		
12	2	44.0	44	
13	6	48.7 ± 2.29	46–54	5.8
		Length of hindfoot		
12	2	15.0	15	
13	6	16.0 ± 0.52	15–17	4.0
		Length of ear		
12	2	13.0	13	
13	6	13.7 ± 0.42	13–14	3.8
		Weight		
12	1	19.0		
13	6	16.2 ± 2.75	13–22	20.9
		Greatest length of skull		
12	2	21.7	21.1–22.3	
13	5	20.4 ± 0.88	21.3–23.9	4.5

Table 5.—*Continued.*

Sample	N	Mean ± 2 SE	Range	CV
		Condylobasal length		
12	2	20.3	19.9–20.7	
13	6	21.0 ± 0.76	20.1–22.5	4.5
		Zygomatic breadth		
12	2	11.1	10.8–11.3	
13	6	11.8 ± 0.38	11.2–12.4	4.0
		Interorbital breadth		
12	2	3.7	3.7	
13	6	3.9 ± 0.16	3.6–4.1	5.0
		Rostral breadth		
12	1	4.1		
13	6	4.2 ± 0.24	3.9–4.7	6.9
		Oblique length of bulla		
12	2	4.7	4.5–4.9	
13	5	4.8 ± 0.23	4.4–5.0	5.3
		Greatest length of bulla		
12	2	7.3	6.9–7.6	
13	5	7.4 ± 0.19	7.1–7.7	2.9
		Length of maxillary toothrow		
12	2	3.7	3.6–3.8	
13	6	3.8 ± 0.12	3.6–4.0	3.9
		Breadth across upper molars		
12	2	5.0	5.0	
13	6	5.3 ± 0.19	5.1–5.7	4.4
		Length of anterior palatal foramen		
12	2	3.8	3.5–4.1	
13	6	4.2 ± 0.18	4.0–4.6	5.3
		Length of posterior palatal foramen		
12	2	0.5	0.4–0.5	
13	4	0.4 ± 0.08	0.3–0.5	20.4
		Length of diastema		
12	2	4.9	4.7–5.0	
13	6	5.3 ± 0.35	4.8–5.9	8.0
		Height of skull		
12	2	7.6	7.5–7.6	
13	6	8.2 ± 0.18	8.0–8.5	2.7
		Length of mandibular toothrow		
12	2	3.1	3.0–3.2	
13	6	3.4 ± 0.12	3.2–3.6	4.5

The holotype of *S. jacksoni* is an individual that is a very old age category III or a young age category IV animal (Table 5, Sample 8). However, even if placed as an age category III individual, it still falls within the normal variation of cranial measurements of *S. caurinus*. Zygomatic breadth of the holotype appears to be relatively narrow even for an age III specimen.

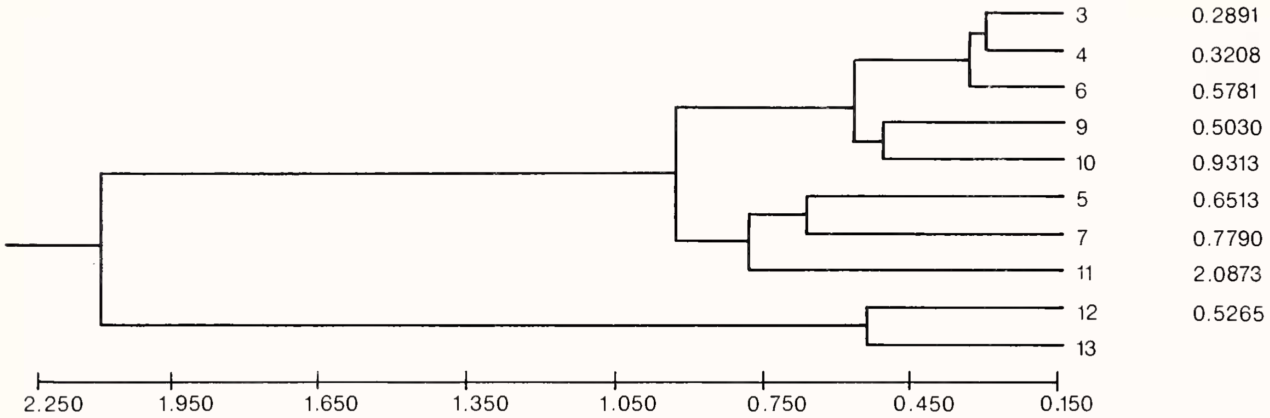

Fig. 3.—Distance phenogram of OTUs (see Fig. 2 and text for key to localities included in each OTU) of West African taxa of *Steatomys* computed from distance matrix based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). OTUs consist of geographic samples of combined sexes. The cophenetic correlation for the phenogram is 0.94.

Multivariate analysis.—Twelve cranial measurements of 10 geographic samples of age category III specimens of combined sexes were analyzed using the NT-SYS routines. Length of posterior palatal foramen and greatest length of skull were excluded from this analysis. Inclusion of greatest length of skull would have caused reduced geographic samples (such as deletion of sample 10) and sample sizes because of missing data.

A distance phenogram diagramming the relationship among 10 geographic samples (OTUs) of *Steatomys* is shown in Fig. 3. The cophenetic correlation coefficient for the phenogram is 0.946. The geographic samples fall into two major clusters. The upper group (OTUs 3, 4, 6, 9, 10, 5, 7, 11) represents medium- to large-sized individuals presently assigned to *S. caurinus*. The lower group represents small individuals from localities in Senegal (OTU 12) and Panisau, Nigeria (OTU 13) and corresponds to the presently recognized *S. cuppedius*.

The first three principal components computed from the matrix of correlation among 12 cranial characters for the same 10 geographic samples (OTUs) are shown in Fig. 4. The proportion of the total phenetic variation accounted for in the first three components is 95.3%. The amounts of variance assigned to each component are 86.9% for component I, 5.2% for component II, and 3.2% for component III. A factor matrix of character loadings among the 12 cranial characters of the principal component analysis is given in Table 6. From the factor analysis it can be seen that the first principal component is heavily influenced by general overall cranial size. The second component is influenced most by length of mandibular toothrow, and the third by interorbital breadth. Examination of the three-dimensional plot (Fig. 4) reveals an expression of phenetic variation similar to that shown in the distance phenogram (Fig. 3); overall cranial size is expressed as progressively larger from left to right. OTUs 12 (Senegal) and 13 (Panisau, Nigeria) cluster on the left, and all other samples cluster in a fairly loose group on the right. Subgroupings within the right cluster of OTUs correspond with those found in the distance phenogram. These subgroupings will be discussed in detail in the systematic accounts that follow.

Taxonomic Conclusions

We interpret the univariate and multivariate analyses to indicate that in West Africa the genus *Steatomys* is represented by three species. Geographically, they are distributed as follows: *Steatomys caurinus* is known from Senegal, Ivory Coast, Upper Volta, Ghana (excluding Wenchi), Togo, Benin, and central Nigeria; *S. cuppedius* from Senegal, northern Nigeria, and south central Niger; and *S. jacksoni* from Wenchi, Ashanti District, Ghana. The latter species is known only from the holotype. *Steatomys cuppedius* is clearly the smallest of the three. *S. jacksoni* and *S. caurinus* are similar in size; the only appreciable difference between them is the size of the interparietal bone, with *S. jacksoni* having a significantly larger one. Little variation in size and shape of this bone is present in all of the

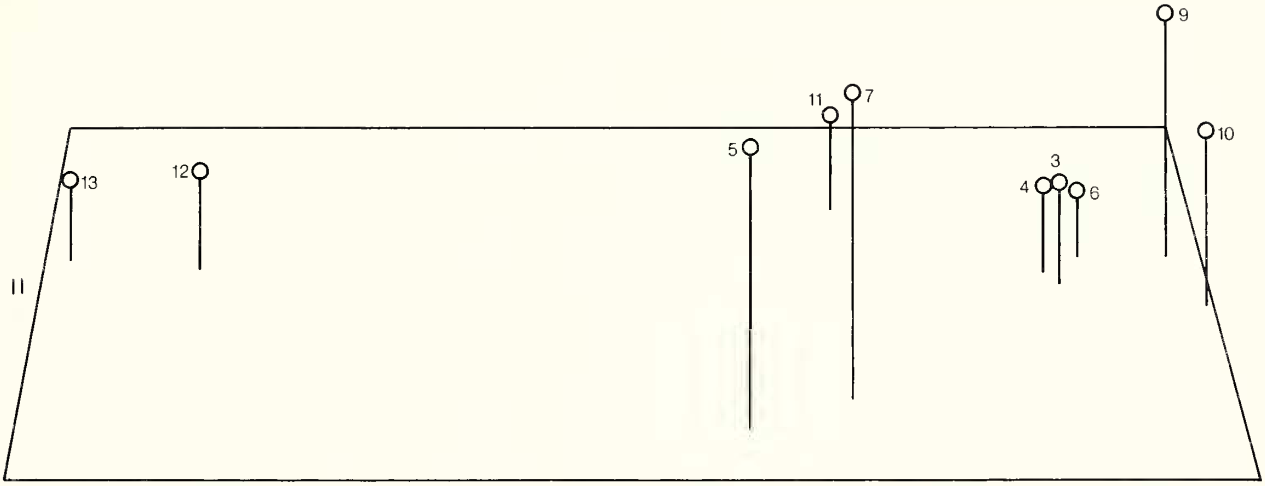

Fig. 4.—Three-dimensional projection of 10 OTUs of West African taxa of *Steatomys* on to the first three principal components based upon a matrix of correlation among 12 cranial measurements. OTUs consist of geographic samples of combined sexes. See Fig. 2 and text for key to localities included in each OTU. Component I accounts for 86.9% of the phenetic variation, component II for 5.2%, and component III for 3.2% for a combined expression of 95.3% of the total variation.

other material examined of the genus from West Africa. The possibility that the holotype of *S. jacksoni* might be an aberrant individual is recognized, but until additional specimens from the vicinity of the type locality of *S. jacksoni* are available for study, we prefer to retain this taxon as a valid species.

Hubert et al. (1973) reported *S. caurinus* from Senegal but presented no measurements. The genus *Steatomys*, with no species given, has also been reported from owl pellets collected from Senegal (Heim de Balsac, 1965, 1967), but once again no measurements were given. The material upon which these reports were based has not been examined by us. We did not have available any *S. caurinus* from Senegal and feel this record should be reexamined to see if the material might be *S. cuppedius*.

SYSTEMATIC ACCOUNTS

Within the following accounts, species and subspecies, if appropriate, are listed in alphabetical order.

Steatomys caurinus Thomas, 1912

Geographic distribution of species.—Central Nigeria, southern Niger, northern Benin, Togo, western Ghana, Upper Volta, central to northern Ivory Coast, and Senegal (Fig. 2); most certainly more widespread and occurring in intervening areas.

Diagnosis.—Large, both externally and cranially, for genus in West Africa; pelage dark and individual hairs coarse; relatively small molars; interparietal bone short in length, usually less than 3.5 mm.

Comparisons.—*Steatomys caurinus* can be distinguished from *S. cuppedius* by a number of characters. Comparisons of greatest length of skull, condylobasal length, greatest length of bulla, and length of diastema show no overlap in measurements of age category III specimens between these two species. These same four characters, and an additional eight measurements, indicate no overlap between age category IV specimens of the two species. These eight are total length, length of ear, weight, zygomatic breadth, rostral breadth, oblique length of bulla, width across upper molars, length of anterior palatal foramen, and height of skull.

Externally, *S. caurinus* can be separated from *S. cuppedius* by dark color of pelage and coarse texture of the hairs as opposed to the pale color of pelage and silky texture of the hairs in the latter species.

From *S. jacksoni, S. caurinus* differs little in ex-

Table 6.—*Factor matrix of character loading of the first three principal components among 12 characters of West African taxa of* Steatomys *(left) and of* Steatomys caurinus *(right).*

Character	*Steatomys* (three species)			*Steatomys caurinus*		
	Component I	Component II	Component III	Component I	Component II	Component III
Condylobasal length	0.996	0.007	−0.021	0.983	−0.076	0.036
Zygomatic breadth	0.958	0.089	−0.053	0.972	0.044	0.032
Interorbital breadth	0.849	−0.027	0.496	0.547	−0.133	−0.619
Rostral breadth	0.980	0.020	−0.089	0.941	0.046	0.146
Oblique length of bulla	0.874	−0.389	−0.244	0.283	0.810	0.424
Greatest length of bulla	0.985	0.043	−0.014	0.921	−0.236	−0.058
Length of maxillary toothrow	0.879	0.248	−0.092	0.568	−0.463	0.511
Breadth across upper molars	0.952	−0.242	0.051	0.692	0.497	−0.315
Length of anterior palatal foramen	0.921	0.154	0.157	0.804	−0.254	−0.315
Length of diastema	0.969	−0.191	−0.093	0.808	0.486	0.233
Height of skull	0.961	−0.169	0.063	0.752	0.289	−0.197
Length of mandibular toothrow	0.845	0.503	−0.139	0.719	−0.608	0.301

ternal or cranial dimensions nor, as far as we can tell, in color of pelage. The single character for distinguishing these two species is the longer length of interparietal bone in *S. jacksoni* than in *S. caurinus*; a length of 4.5 mm in the former versus less than 3.5 mm, in fact except for a few individuals, less than 3.0 mm in the latter.

Geographic Variation

Univariate analysis.—In examining geographic variation in *S. caurinus*, five external and 14 cranial measurements of age category III individuals were examined and the following results were found (Table 4). The specimens of the combined geographic sample from Yama and Sienso (OTU 11) of northwestern Ivory Coast are clearly smaller than are those of all of the other geographic samples tested in nine of the 19 characters examined. These nine characters are total length, greatest length of skull, condylobasal length, zygomatic breadth, rostral breadth, oblique length of bulla, width across upper molars, length of diastema, and height of skull.

The geographic sample from Tyenko (OTU 9), which is less than 100 mi south of OTU 11, and that from Diali (OTU 10), which is from still farther south and east in Ivory Coast than OTU 9, are both clearly larger than are the remaining geographic samples of *S. caurinus* examined in total length, length of tail, greatest length of skull, condylobasal length, length of anterior palatal foramen, and height of skull. OTUs 9 and 10 are even more strikingly large when compared with OTU 11, the geographic sample exhibiting the smallest dimensions for the species. Three specimens were available for study from Diali (OTU 10); two of these specimens were large for the species. Diali and also the type locality of *S. jacksoni* (Wenchi, Ghana) are situated on the interface of the High forest and Invasive woodland in West Africa. The holotype of *S. jacksoni* and the two large specimens from Diali are comparable in size, except for length of interparietal.

There is no indication of a trend in variation in hindfoot length although OTU 3 (Pirisi, Ghana) and OTU 4 (Gudi, Nigeria) tend to have relatively long hindfeet when compared to the other geographic samples. The same discordant pattern is apparent in the variation in the length of the ear, although there is no clear grouping of geographic areas into different size groups, OTU 11 displayed relatively long ears. In both instances, this discordance could be an artifact of different techniques used by preparators of skins. The cranial characters of interorbital breadth, length of maxillary toothrow, length of posterior palatal foramen, and length of mandibular toothrow show little geographic variation.

Considering the vast distances involved (about 1200 km), the geographic samples from OTU 3 in Ghana, OTU 6 in Upper Volta, and OTU 4 in Nigeria show little geographic variation in the characters tested.

Multivariate analysis.—Twelve cranial measurements of eight geographic samples of age category III specimens of combined sexes were analyzed using the NT-SYS routines. Again the length of posterior palatal foramen and greatest length of skull were excluded from the analysis. A distance phe-

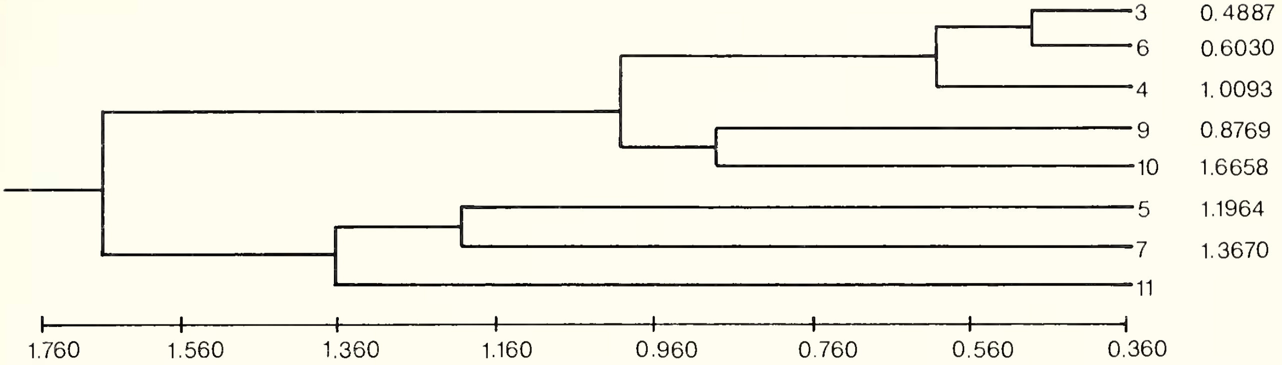

Fig. 5.—Distance phenogram of OTUs (see Fig. 2 and text for key to localities included in each OTU) of *Steatomys caurinus* computed from distance matrix based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). OTUs consist of geographic samples of combined sexes. The cophenetic correlation for the phenogram is 0.87.

nogram showing the relationship among eight geographic samples of *Steatomys caurinus* is illustrated in Fig. 5. The cophenetic correlation coefficient for the phenogram is 0.87. The OTUs separate into two major groups. The upper one (OTUs 3, 6, 4, 9, and 10) includes individuals of medium to large cranial dimensions. This group further clusters into two subgroups—OTUs 9 (Tyenko) and 10 (Diali) from the Ivory Coast are included in one subgroup, and OTUs 3 (Pirisi, Ghana), 4 (Gudi, Nigeria), and 6 (Cella, Upper Volta) in a second subgroup. Of these two subgroups, the former subgroup consists of the larger sized individuals of the two subgroups. Although OTUs 9 and 10 are paired together on the phenogram, they are well separated by phenetic distance. The lower major group consists of three OTUs paired together but well separated by phenetic distance; OTUs 5 and 7 from Upper Volta, and OTU 11 from Yama and Sienso, Ivory Coast.

The first three principal components computed from the matrix of correlation among 12 cranial characters for eight geographic samples (OTUs) of *Steatomys caurinus* are presented in Fig. 6. The amount of phenetic variation represented in each of the first three components is 60.1% for component I, 16.3% for component II, and 10.2% for component III, for a total expression of 86.6% of the total phenetic variation. A factor matrix of character loadings from correlation among the 12 cranial characters is given in Table 6. From Table 6, it can be seen that the first, and by far the most important, component is heavily influenced by general cranial size; especially those measurements expressing length of skull, breadth of zygoma and rostrum, and greatest length of bulla. Interorbital breadth, oblique length of bulla, and length of maxillary toothrow show relatively low values for component I. Component II is influenced positively by oblique length of bulla and negatively by length of mandibular toothrow, whereas component III has a high positive value for length of maxillary toothrow and a high negative value for interorbital breadth.

Examination of the three-dimensional plot of the principal components (Fig. 6) reveals a pattern of variation in accordance with that shown in the distance phenogram (Fig. 5). OTUs 5, 7, and 11 form one main group on the left, with each OTU distantly separated from each other. The other major grouping, consisting of OTUs 3, 4, 6, 9, and 10 forms two subclusters with OTUs 3, 4, and 6 constituting the one and OTUs 9 and 10 the other.

This projection plot indicates that OTU 11 consists of individuals with small overall cranial size, especially with short and narrow skulls (Table 6). Although the overall length of bulla, including mastoidal portion, is long, the audital portion, as expressed in component II, is shortened. Component II also indicates a relatively long mandibular toothrow compared to OTUs 5 and 7. Interorbital breadth of individuals of OTU 11 is narrow as shown by the negative influence of this character on component III. Component III indicates a long maxillary toothrow for OTU 11.

OTUs 5 and 7 from Upper Volta are small in overall size. Both are well separated from OTU 11 in components II and III by the characters mentioned above. In spite of having generally short and narrow skulls, their scores for component III indicate a relatively broad interorbital region and short maxillary toothrow, the latter corresponding with

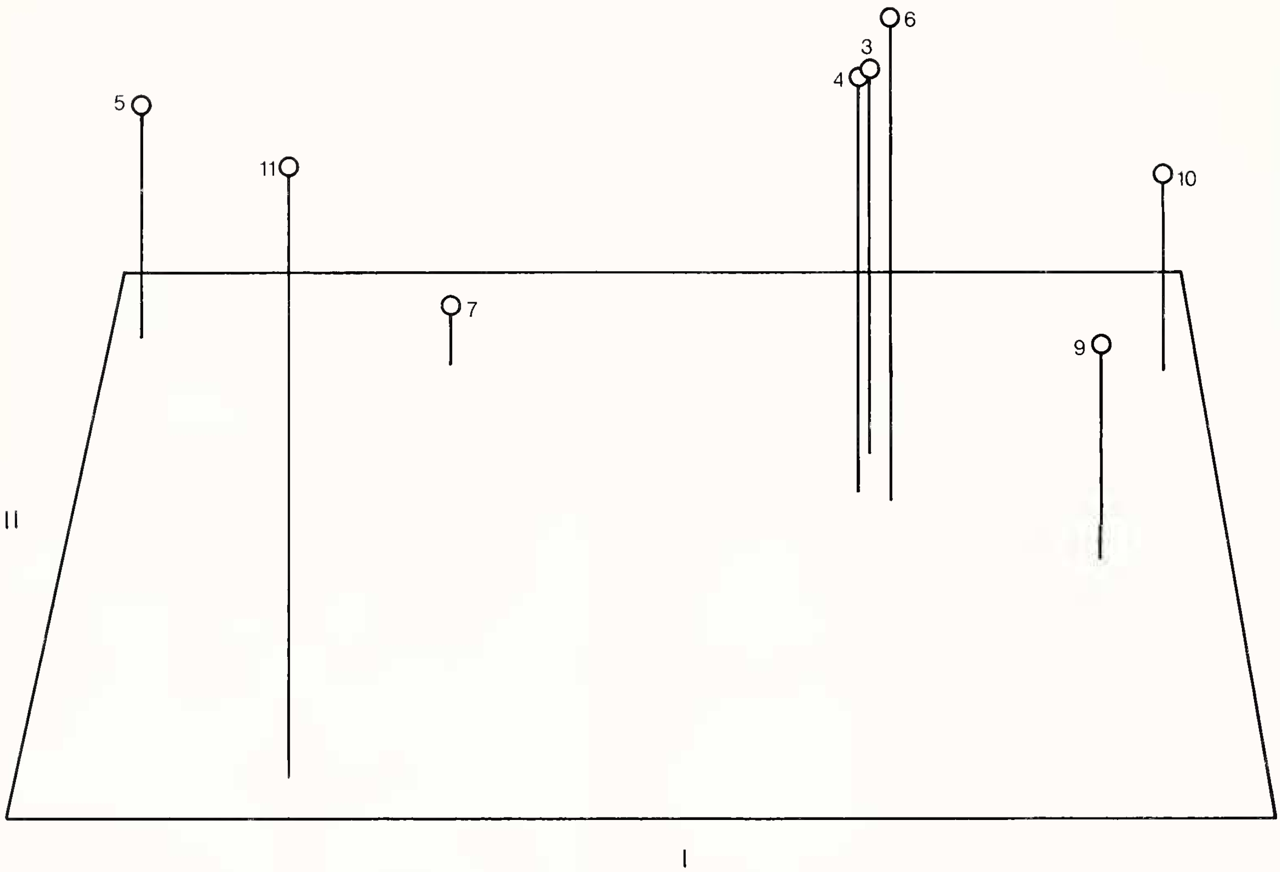

Fig. 6.—Three-dimensional projection of eight samples of *Steatomys caurinus* on to the first three principal components based upon a matrix of correlation among 12 cranial measurements. OTUs consist of geographic samples of combined sexes. See Fig. 2 and text for key to localities included in each OTU. Component I accounts for 60.1% of the phenetic variation, component II for 16.3%, and component III for 10.2% for a combined expression of 86.6% of the total variation.

their short mandibular toothrow as expressed on component II.

The other geographic samples from Ivory Coast (OTUs 9 and 10), represented by a maximum of five and three specimens, respectively, contain large individuals. These OTUs are essentially equal in skull dimensions as expressed in components I and III, but separate somewhat based on component II—an expression of length of auditory bulla and, inversely, length of mandibular toothrow.

The OTUs 3, 4, and 6 are all represented by large sample sizes (minimum of 18 specimens), and are morphologically identical even though 1,200 km separate OTU 3 from 4. Other than slight differences in overall size of skull, and slightly narrower interorbital region and longer maxillary toothrow, OTUs 3, 4, and 6 differ little from OTUs 9 and 10.

Taxonomic Conclusions

Based on our assessment of geographic variation, we have separated *S. caurinus* into two taxonomically recognizable populations. The smallest individuals in the species belong to the population from Yama and Sienso in northwestern Ivory Coast and are herein described as a new subspecies. A second subspecies, *S. caurinus caurinus* Thomas, 1912, represented by mice of medium to large size, is known from Tyenko and Diali, Ivory Coast, Upper Volta, Ghana, Togo, Benin, and Nigeria. OTUs 2 and 6 from Upper Volta represent relatively small individuals, but, considering the small sample sizes and geographic distribution of the OTUs involved, is retained in *S. c. caurinus*. Further samples are required from within the areas between the Yama and Sienso (Ivory Coast) localities and Ghana

(OTU 2) and Upper Volta (OTUs 5 and 7) populations in order to determine the distribution of the new subspecies and its relationships to the populations at the latter localities. Also the taxonomic and distributional status of the individuals of large size from Tyenko (OTU 9) and Diali (OTU 10), Ivory Coast, is deserving of additional study.

Steatomys caurinus caurinus Thomas, 1912

1912. *Steatomys caurinus* Thomas, Ann. Mag. Nat. Hist., ser. 9, 9:271, February.

1977. *Steatomys pratensis caurinus*, Coetzee, *in* Meester and Setzer (eds.), The mammals of Africa . . . , Smithsonian Inst. Press, 6–8:1–4.

Holotype.—Young adult female (age category III), skin and skull BMNH 12.1.16.24, from Panyam, 4,000 ft, Nigeria; obtained 13 July 1911 by Rev. G. T. Fox, original number 47. Skin in good condition; skull with left occipital region broken, both bullae separated from skull but repaired with glue, left zygoma broken.

Measurements of holotype.—Total length, 164; length of tail, 54; length of hindfoot, 19; length of ear, 19; greatest length of skull, 27.3; interorbital breadth, 3.9; rostral breadth, 4.8; length of maxillary toothrow, 4.0; breadth across upper molars, 6.1; length of anterior palatal foramen, 5.0; length of diastema, 7.2; length of mandibular toothrow, 3.4.

Distribution.—Known from Ivory Coast (Tyenko and Diali), Upper Volta, western and northern Ghana, northern Togo and Benin, and central Nigeria. Literature records indicate its occurrence in Senegal as well.

Comparisons.—For comparisons of *Steatomys caurinus caurinus* with other taxa from West Africa, see each of the following accounts.

Remarks.—The subspecies *S. c. caurinus* consists of individuals of medium to large size for the species and seems to occur over an extensive geographic area from at least Ivory Coast east to Nigeria, although originally known only from Nigeria (Thomas, 1912*a*, 1912*b*). Within this area, specimens are generally uniform in size and in shape of skull. In the Ivory Coast, specimens of two sizes have been reported by Heim de Balsac (1967). For additional comments on this material, see the following account.

Steatomys caurinus was reported from Bandia, Senegal, by Hubert et al. (1973). Heim de Balsac (1967:219) reported a large and a small *Steatomys* from M'Bour, Senegal. We are accepting both locality records as *S. caurinus* at this time but are unable to assign with certainty this material to subspecies. Because the relationship of the Senegalese specimens could well be to the populations of the Sudan Woodland of Upper Volta, we are listing the literature records under the nominate subspecies. Based on these published reports, it appears that the only locality of sympatry between *S. caurinus* and *S. cuppedius* in West Africa would be M'Bour, Senegal.

Specimens examined (196).—BENIN: Kouande, 1 (USNM). GHANA: Bawku, 1,400 ft, 1 (BMNH); Bangwon, 5 (USNM); Pirisi, 43 (USNM); Sakpa, 1 (USNM). IVORY COAST: Bouna, 1 (USNM); Diali, 14 (USNM); Tyenko, 12 (USNM). NIGERIA: 3 mi E Gudi, 52 (USNM); Panyam, 4,000 ft, 11 (BMNH). TOGO: Dapango, 1 (USNM); 1 km N Cella, 48 (USNM); Dio, 1 (USNM); Fo, 1 (USNM); 36 mi SE Nayoure, 1 (USNM).

Additional records.—IVORY COAST: Lamto (Bellier, 1967; Heim de Balsac and Bellier, 1967:159; Bellier and Gatun, 1968:708, Heim de Balsac, 1967:215–219); Bouake (Heim de Balsac, 1967; Heim de Balsac and Bellier, 1967:159; Bellier and Gatun, 1968:708). SENEGAL: Bandia (Hubert et al., 1973:81), M'Bour (Heim de Balsac, 1967:219).

Steatomys caurinus roseveari, new subspecies

Holotype.—Adult male, skin and skull, USNM 467496, from Yama, Ivory Coast; obtained on 22 March 1969 by L. W. Robbins, original number 1106. Skin in good condition, missing left front foot; skull in good condition, nasals damaged.

Measurements of holotype.—Total length, 156; length of tail, 47; length of hindfoot, 18; length of ear, 17; weight, 42 g; condylobasal length, 25.3; zygomatic breadth, 13.0; interorbital breadth, 4.1; rostral breadth, 5.0; oblique length of bulla, 5.5; greatest length of bulla, 9.1; length of maxillary toothrow, 4.2; breadth across upper molars, 5.8; length of anterior palatal foramen, 5.6; length of posterior palatal foramen, 0.4; height of skull, 9.9; and length of mandibular toothrow, 3.2. Additional measurements are listed in Tables 3, 4, and 5.

Distribution.—At present known only from Sienso and Yama in northwestern Ivory Coast.

Comparisons.—*Steatomys caurinus roseveari* can be distinguished from *S. c. caurinus* by its smaller size, especially cranial dimensions. Most characteristic of this new subspecies are short and narrow skulls with relatively narrow interorbital region and long maxillary and mandibular toothrows. From *S. jacksoni* and *S. cuppedius*, *S. c. roseveari* can be separated as for the species.

Remarks.—Heim de Balsac (1967) considered the taxonomic status of *Steatomys* in the Ivory Coast but failed to put specific epithets on his specimens. Heim de Balsac (1967:216–220) reported large and small specimens from Bouake and Lamto. Without having examined these specimens, we are unable to make a definitive judgment. It is possible these differences are attributable to nongeographic variation such as age (certainly at least specimens A and D in figure 14 of Heim de Balsac, 1967, are young animals) or there might be two distinct taxa represented. *S. caurinus roseveari* is smaller than the nominate subspecies. The small form reported by Heim de Balsac (1967) might represent this new subspecies. If this were true, and it was sympatric with *S. caurinus caurinus,* then each must be recognized as distinct species. In the geographic sample from Tyenko (OTU 9) or Diali (OTU 10) we could not find any evidence of intergradation or of two distinct morphotypes being present. For now we consider these small individuals from Tyenko and Diali to be a subspecies of *S. caurinus.*

Etymology.—This new subspecies is named for D. R. Rosevear who has contributed much, both in the field and in print, to the study of the mammals of West Africa. His monumental written contributions will serve for many years as a primary reference for anyone interested in bats, rodents, or carnivores of this fascinating region of Africa. For his abundant contributions after his retirement and return to England from Nigeria, all who study small mammals in West Africa owe him a large amount of gratitude.

Specimens examined (75).—IVORY COAST: Sienso, 6 (USNM); Yama, 69 (USNM).

Steatomys cuppedius Thomas and Hinton, 1920

Geographic distribution of species.—Known from northern Nigeria, southern Niger, and Senegal.

Diagnosis.—Small, both externally and cranially, for the genus in West Africa; condylobasal length of skull less than 20.7 mm; length of maxillary toothrow usually less than 4.0 mm; pelage pale in color, with individual hairs soft.

Comparisons.—From all other species of *Steatomys* occurring in West Africa, *S. cuppedius* can be separated by its small size, both externally and cranially. Skulls of *S. cuppedius* are less than 20.7 mm in condylobasal length in age category III individuals.

Geographic Variation

Univariate analysis.—Five external and 14 cranial measurements of age category III individuals of *Steatomys cuppedius* from Senegal and Nigeria were examined for geographic variation. The geographic sample from Senegal is larger in size than is the one from Nigeria (Table 4). Of age category III individuals, four measurements (total length, weight, greatest length of skull, and oblique length of bulla) of the populations from Senegal were significantly larger than those from Nigeria. Nine other measurements averaged larger and four averaged smaller, whereas two were equal in size (Table 4). Only small samples of age category IV were available for analysis of geographic variation (Table 5). A trend similar to that found in age category III is not indicated in such small samples.

Taxonomic Conclusions

Only three geographic samples of *S. cuppedius* were examined—a single individual from Niger and two geographic samples of sizeable proportions from Senegal and Nigeria. Considering the distance of approximately 2,500 km between the geographic samples from Senegal and Nigeria, the geographic variation present is not striking. Taxonomic separation of these localities is not warranted; we consider *Steatomys cuppedius* to be a monotypic species.

Steatomys cuppedius Thomas and Hinton, 1920

1920. *Steatomys cuppedius* Thomas and Hinton, Novit. Zool., 27:318, 15 June.

1977. *Steatomys parvus cuppedius,* Coetzee, *in* Meester and Setzer (eds.), The mammals of Africa . . . , Smithsonian Inst. Press, 6.8:1–4.

Holotype.—Adult female (age category IV), skin and skull, BMNH 21.2.11.85, from Farniso (=Panisau), near Kano, 1,700 ft, Nigeria; obtained 29 December 1919 by A. Buchanan, original number 70. Skin in good condition; skull in fair condition, left zygoma broken.

Measurements of holotype.—Total length, 124; length of tail, 43; length of hindfoot, 14; length of ear, 14; greatest length of skull, 21.3; condylobasal length, 20.4; interorbital breadth, 3.6; rostral breadth, 4.2; greatest length of bulla, 7.7; breadth across upper molars, 5.2; length of anterior palatal foramen, 8.8; length of diastema, 5.2; height of skull, 8.0; length of mandibular toothrow, 3.0.

Distribution.—This species is known from central Nigeria, Niger, and Senegal.

Comparisons.—See comparisons for species.

Remarks.—Originally described from material from northern Nigeria (Thomas and Hinton, 1920, 1921), *Steatomys cuppedius* has been uncommon in collections of rodents from West Africa. Thomas (1925:194) reported a single specimen from Gangara, Niger, a locality across the Nigerian border to the northeast from the type locality. Although large numbers of *Steatomys* from Upper Volta were available, none proved to be *S. cuppedius*. If the latter occurs in Upper Volta, it will probably be found in the extreme north and have a distribution similar to *Gerbillus nigeriae*, as it seems to have in Nigeria.

There seems to be some doubt as to the identity of the skulls reported from owl pellets by Heim de Balsac (1965). Later, Heim de Balsac and Bellier (1967) indicate that the material from "nord de Saint-Louis du Senegal" and "au voisinage de M'Bour" was smaller than the material obtained in Ivory Coast. If this is true, it is likely this Senegalese material belongs to *S. cuppedius* although we are unable to identify it with certainty. We have included these records under the additional records of this species.

Specimens examined (113).—NIGER: Gangara, 1,400 ft, 1 (BMNH). NIGERIA: Farniso, near Kano, 1,700 ft, 6 (BMNH); Panisau, 55 (USNM). SENEGAL: 17 km NE Kiourbel, 1 (USNM); 15 km N Karrfine, 16 (USNM); 6 km E Kaolack, 7 (USNM); Koungheul, 27 (USNM).

Additional records.—SENEGAL: north of St. Louis, (Heim de Balsac, 1967:219; Heim de Balsac and Bellier, 1967:159); M'Bour (Heim de Balsac and Bellier, 1967:159).

Steatomys jacksoni Hayman, 1936

Geographic distribution of species.—Known only from the type locality, Wenchi, Ashanti [district], Ghana.

Diagnosis.—Size large, both externally and cranially, for genus in West Africa; skull long and relatively narrow; interparietal bone long, 4.5 mm in length.

Comparisons.—For comparisons with *S. cuppedius* and *S. caurinus*, see accounts of that species and for additional comments, see section "Relationships of Species."

Steatomys jacksoni Hayman, 1936

1936. *Steatomys jacksoni* Hayman, Proc. Zool. Soc. London, for 1935, pp. 930, 10 January.

1977. *Steatomys pratensis jacksoni*, Coetzee, *in* Meester and Setzer (eds.), The mammals of Africa . . . , Smithsonian Inst. Press, 6.8:1–4.

Holotype.—Young adult male (young age category IV), skin and skull BMNH 35.1.30.157, from Wenchi, Ashanti, Ghana; obtained 18 January 1934 by W. P. Lowe, original number 104. Skin and skull in good condition.

Measurements of holotype.—Total length, 170; length of tail, 50; length of hindfoot, 18; length of ear, 18; greatest length of skull, 28.5; condylobasal length, 27.1; zygomatic breadth, 12.9; interorbital breadth, 4.0; rostral breadth, 5.3; oblique length of bulla, 5.8; greatest length of bulla, 9.6; length of maxillary toothrow, 4.0; breadth across upper molars, 6.1; length of anterior palatal foramen, 5.7; length of diastema, 7.2; height of skull, 10.0; length of mandibular toothrow, 3.7.

Distribution.—Same as given above.

Comparisons.—See comparisons given above.

Remarks.—We prefer to retain this taxon as a valid species based solely on the size and shape of the interparietal bone. Additional material from the type locality is required before a critical evaluation of variation in the interparietal bone can be made.

Specimens examined (1).—GHANA: Wenchi, Ashanti, 1 (BMNH).

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We are indebted to the following institutions and curators who made available West African *Steatomys* specimens for study. Abbreviations preceding the names of institutions are used in the accounts above to identify the source of specimens.

BMNH—British Museum (Natural History), London (I. Bishop).

USNM—United States National Museum of Natural History, Smithsonian Institution, Washington, D. C. (Henry W. Setzer).

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GAZETTEER

Names of geographic features listed below are those used in the text. The primary sources for spellings and coordinates of localities were the individual specimen tags and the gazetteers of the United States Board on Geographic Names (prepared by the Office of Geography, Department of Interior).

Benin:	Kouande	10 20 N, 01 41 E
Ghana:	Bangwon	10 58 N, 02 41 W
	Bawku	11 05 N, 00 11 W
	Pirisi	10 07 N, 02 27 W
	Sakpa	08 52 N, 02 21 W
	Wenchi	07 45 N, 02 02 W
Ivory Coast:	Bouake	07 41 N, 05 02 W
	Bouna	09 16 N, 03 00 W
	Diali	07 03 N, 05 37 W
	Katiola	08 08 N, 05 06 W
	Lamto	06 12 N, 04 58 W
	Ouango Fitini	09 34 N, 04 03 W
	Sienso	09 25 N, 07 31 W
	Tyenko	08 14 N, 07 24 W
	Yama	09 36 N, 06 19 W
Niger:	Gangara	ca. 14 00 N, 09 00 E
Nigeria:	Farniso [=Panisau]	
	Gudi	08 54 N, 08 17 E
	Panisau (Panisa)	11 43 N, 07 32 E
Senegal:	Bandia	14 37 N, 17 02 W
	Diourbel	14 40 N, 16 15 W
	Kaffrine	14 06 N, 15 33 W
	Kaolack	14 06 N, 16 33 W
	Koungheul	13 59 N, 14 48 W
	M'Bour	14 24 N, 16 58 W
	St. Louis	16 02 N, 16 30 W
Togo:	Dapango	10 52 N, 00 13 E
	Wulehe	08 40 N, 00 00
Upper Volta:	Barga	13 51 N, 02 12 W
	Cella	11 38 N, 00 22 W
	Dio	13 20 N, 02 38 W
	Fo	11 53 N, 04 31 W
	Nayoure	12 15 N, 00 16 E

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A CRITICAL EXAMINATION OF ALLEGED SIBLING SPECIES IN THE LESSER THREE-TOED JERBOAS (SUBGENUS *JACULUS*) OF THE NORTH AFRICAN AND ARABIAN DESERTS

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ABSTRACT

Alleged sibling speciation in the lesser three-toed jerboas is considered. Variation in supposed diagnostic characters is examined. *Jaculus deserti* Loche, 1867, is shown to be a junior synonym of *J. jaculus* Linnaeus, 1758.

INTRODUCTION

Ellerman and Morrison-Scott (1951) in their comprehensive review of Palaearctic mammals recognized only three species of this subgenus, namely *Jaculus jaculus* Linnaeus, 1758, *Jaculus blanfordi* Murray, 1884, and *Jaculus orientalis* Erxleben, 1777. The validity of these three taxa is not in doubt, but recently the suggestion has been made (Ranck, 1968) that two sibling species exist within the populations of the lesser three-toed jerboa, *Jaculus jaculus,* occurring in northern Africa and the Arabian Peninsula. For one of these sibling species Ranck (1968) has employed an old taxon, *Jaculus deserti*, based on *Dipus deserti* Loche, 1867.

Ranck (1968) keyed these two species as follows:

Dorsal color dark; two foramina on angular process of mandible; sole of hind foot and matatarsal area suffused with brownish hairs .... *J. deserti*

Dorsal color pale; a single foramen on angular process of mandible; sole of hind foot and metatarsal area white or buff and lacking suffusion of brownish hairs .... *J. jaculus*

Ranck (1968) gave the range of his *J. deserti* as Arabia, Iraq, Israel, Sinai, Egypt, Libya, and Algeria and referred the following taxa as subspecies of it: *J. deserti deserti* Loche, 1867; *J. deserti vastus* Ranck, 1968; *J. deserti rarus* Ranck, 1968; *J. deserti fuscipes* Ranck, 1968; *J. deserti favillus* Setzer, 1955; *J. deserti schluteri* Nehring, 1901; *J. deserti vocator* Thomas, 1921; and *J. deserti loftusi* Blanford, 1875.

For *Jaculus jaculus* Ranck (1968) gave the general range as Iraq, Syria, Lebanon, Israel, Jordan, Saudi Arabia, and North Africa south through the Sahara including Sudan, Chad, Niger, Mauritania, and Spanish Sahara. To this species Ranck referred the following taxa: *Jaculus jaculus jaculus* Linnaeus, 1758; *J. jaculus arenaceous* Ranck, 1968; *J. jaculus collinsi* Ranck, 1968; *J. jaculus cufrensis* Ranck, 1968; *J. jaculus tripolitanicus* Ranck, 1968; *J. jaculus whitchurchi* Ranck, 1968; *J. jaculus sefrius* Thomas and Hinton, 1921; *J. jaculus centralis* Thomas and Hinton, 1921; *J. jaculus butleri* Thomas, 1922. Other subspecies not specifically allocated by Ranck include *J. jaculus airensis* Thomas and Hinton, 1921; *J. jaculus favonicus* Thomas, 1913; *J. jaculus gordoni* Thomas, 1903; and *J. jaculus vulturnus* Thomas 1913.

Harrison (1972), reviewing the material of *Jaculus* from the Arabian Peninsula, has already thrown doubt on the validity of these "sibling species," stating "I am quite unable to distinguish two small species of *Jaculus* in the extensive Arabian material examined . . . individual variation in both coloration of the soles and size and number of the angular foramina is so extensive and random in the Arabian jerboas that the definition of two species on this basis appears quite impossible."

As a preliminary part of an extended investigation of geographical variation in *Jaculus*, it appeared necessary to make a critical examination of Ranck's sibling species criteria in North African as well as in the Arabian populations, in order to evaluate the problem more fully and prevent further systematic confusion. That is the purpose of the present study, which is not intended in any other way as a revision of the numerous geographical forms listed above. Such a revision must clearly await far more detailed and extensive research.

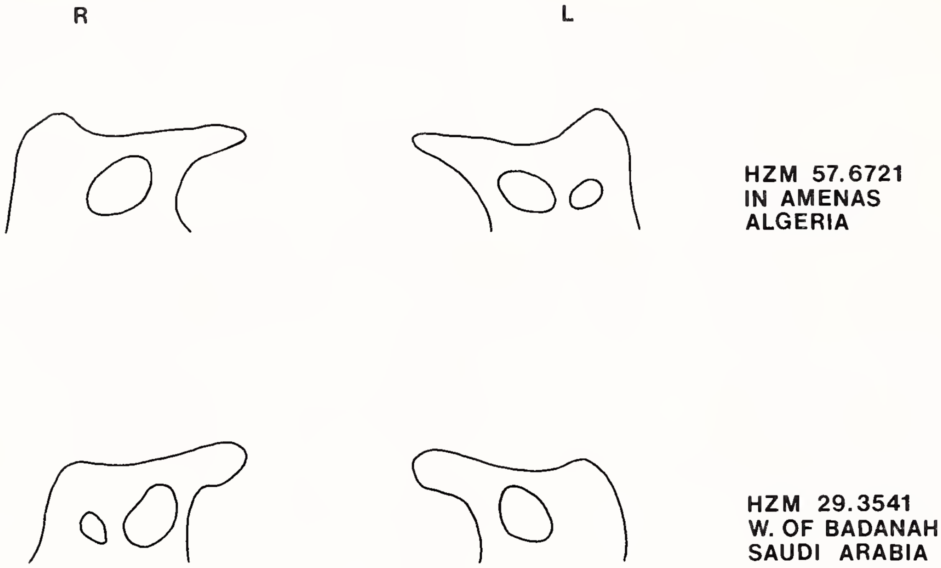

Fig. 1.—Examples of the angular processes of two specimens of *Jaculus jaculus* from Algeria and Saudi Arabia showing variation in angular foramina. Angular formina scores are 1 - 2 above and 2 - 1 below. Abbreviations are R (right) and L (left); numbers are registry numbers for specimens in the Harrison Zoological Museum (HZM).

METHODS

Coloration

Of the characters employed by Ranck to separate *J. deserti* and *J. jaculus*, both dorsal coloration and sole coloration are necessarily somewhat subjective, but have been found susceptible to the method of scoring listed below, in each specimen examined:

Dorsal coloration

1. Pallid sandy	Paler
2. Grayish sandy	↓
3. Brownish sandy	Darker

Sole coloration

1. White	Paler
2. Buff	↓
3. Brown	Darker

A major source of confusion has been found to occur in the case of sole coloration in *Jaculus*, namely discoloration of the sole and digital brushes by the substrate. A most striking example of this was seen in a series of skins from In Amenas, Algeria, in which the soles and digital brushes are bright orange—until washed with water, when the orange discoloration disappears, leaving a white condition. With experience it is usually possible to distinguish discoloration from true pigmentation and washing is seldom required.

Angular Foramina

Fortunately, the angular foramina are easily evaluated and can be counted and recorded with stereomicroscopic drawings. Unfortunately, the angular process is delicate and hence often broken in preparation. It is pertinent to observe here that the angular foramina represent unossified areas in bone, which are occupied by membrane in life, a fact which no doubt accounts for their great variability, both in size and number.

These criteria have been recorded for each specimen examined and the results are summarized below in tabular form with all Arabian material and all North African material arranged in two separate groups. In these tables the scores for each specimen are arranged with dorsal coloration, sole coloration, and foramen counts for the right and left mandible in series from left to right, thus a score of 2:2:2-2 would indicate an animal with intermediate coloration of the dorsum and soles and two angular foramina on each side. The results are simply expressed as the number of individuals from each group showing each numerical score (where a mandibular foramen is broken or absent it is scored as x). Only those specimens able to provide a combination of dorsal and sole coloration with one or both angular foramen counts are included in this study; skins without skulls and skulls without skins are excluded. Each score is listed as being compatible (COM), incompatible (NC), or intermediate (INT).

RESULTS AND DISCUSSION

It is clear that if Ranck's hypothesis of two sibling species is correct, based on the characters given in his key, then both in African and Arabian populations two groups of scores ought to predominate in these results:

3 : 3 : 2 - 2
3 : 2 : 2 - 2
2 : 3 : 2 - 2

indicating the *deserti* species with dark or darkish dorsum and soles and two angular foramina. On the other hand, the following scores:

1 : 1 : 1 - 1
2 : 1 : 1 - 1
1 : 2 : 1 - 1

would indicate the *jaculus* species with pallid or palish dorsum and soles but one angular foramen.

Table 1.—*Scores obtained in this study for dorsal coloration, sole coloration, and angular foramina counts of* Jaculus. *Number of individuals with each score is indicated for each continent. COM = compatible, NC = not compatible, and INT = intermediate scores for Ranck's decision.*

Compatibility	Score	Arabian Peninsula	Africa
COM	1:1:1 - 1	4	2
COM	1:1:X - 1	2	2
COM	1:1:1 - X	0	2
NC	1:1:1 - 2	2	0
NC	1:1:2 - 2	1	0
NC	1:1:2 - X	1	1
NC	1:1:X - 2	1	2
COM	1:2:1 - 1	1	19
COM	1:2:X - 1	0	4
COM	1:2:1 - X	0	1
NC	1:2:1 - 2	0	4
NC	1:2:2 - 1	0	3
INT	1:2:2 - 2	4	16
INT	1:2:2 - X	2	6
INT	1:2:X - 2	3	5
INT	1:2:2 - 3	0	3
INT	1:2:3 - 3	0	1
INT	1:2:2 - X	0	2
INT	1:3:2 - 2	0	2
INT	1:3:2 - X	1	2
NC	1:3:1 - X	1	0
INT	2:2:1 - 1	5	4
INT	2:2:X - 0	1	0
INT	2:2:X - 1	3	3
INT	2:2:1 - X	3	0
NC	2:2:1 - 2	1	0
NC	2:2:1 - 3	0	2
INT	2:2:2 - 2	8	5
INT	2:2:2 - X	5	0
INT	2:2:X - 2	5	4
NC	2:2:2 - 1	2	2
INT	2:2:3 - 2	1	1
INT	2:1:2 - 2	2	0
INT	2:1:2 - X	1	0
COM	2:3:2 - 2	2	0
COM	2:3:2 - X	2	0
COM	2:3:X - 2	2	0
NC	2:3:X - 1	1	0
COM	3:3:X - 2	0	1
NC	3:2:2 - 1	0	1

On the other hand, scores including angular foramen counts of 2 - 1 or 1 - 2 ought not to occur at all, indicating both species foramen count in one individual (Fig. 1), and scores of

1 : 1 : 2 - 2
3 : 3 : 1 - 1

similarly should not occur at all, whereas the occurrence of many intermediate scores must cast further doubt on the validity of the hypothesis.

In both African and Arabian jerboas, scores for the angular foramina of 1 - 2 and 2 - 1 occur with such frequency (Table 1, Fig. 1) that on this consideration alone the sibling species hypothesis as advanced by Ranck simply cannot be upheld. Furthermore, the predicted scores for the two species do not predominate; other incompatible scores also occur at an unacceptable high incidence and intermediate scores form the highest percentage in both populations. The number of individuals assessed and percentage occurrences of compatible, incompatible, and intermediate scores are given in Table 2.

Table 2.—*Summary of compatibility results for* Jaculus *from Table 1.*

	Arabia		Africa	
Compatibility	Number	Percentage	Number	Percentage
Compatible	13	19	31	31
Incompatible	10	15	15	15
Intermediate	44	66	54	54
Total	67		100	

CONCLUSIONS

It is suggested that the number of angular foramina in *Jaculus* is a matter of random individual variation, often differing in the two mandibles of an individual. It is further suggested that pallid or darker dorsal coloration and sole brushes are in reality related to substrate coloration in *Jaculus* and represent the effect of selection in producing "substrate races" more or less protected by cryptic resemblance to the predominant substrate, as has been well demonstrated in the three-toed jerboa and many other desert rodents (Harrison, 1975). The concept of two sibling species within *Jaculus jaculus* populations on the basis proposed by Ranck (1968) is rejected.

ACKNOWLEDGMENTS

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ENERGETICS OF SURVIVAL IN *HETEROCEPHALUS GLABER* (RÜPPELL), THE NAKED MOLE-RAT (RODENTIA: BATHYERGIDAE)

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ABSTRACT

Heterocephalus glaber, a colonial mole-rat, has a highly structured social system with a worker and non-worker class and a dominant breeding female. Recruitment rates for the colony and growth rates of the young are very low. Unusual features in its physiology (a high rate of thermal conductance, a low basal metabolic rate, a low body temperature, and poor ability to thermoregulate) have in the past been regarded solely as adaptations to the high temperature and humidity of the burrows in which mole-rats live. It is here suggested that food is limiting to *Heterocephalus* and that many of its unusual features can be attributed to the need to maintain a low energy budget for the colony.

INTRODUCTION

Heterocephalus glaber, the naked mole-rat is a small colonial rodent with an average weight of about 35 g. It occurs in arid regions of Kenya, Ethiopia, and Somalia—areas characterized by a low mean annual temperature amplitude, diurnal ambient temperatures of above 27°C, and an annual rainfall of less than 700 mm. Vegetation in these areas is sparse and many plants have swollen subterranean portions; these form the main food for *Heterocephalus.*

Heterocephalus lives underground in a burrow system, which consists of extensive foraging burrows running at root or tuber level and a deeper nest area. The ground is very hard and the burrows semipermanent (Jarvis and Sale, 1971). The tubers and bulbs, on which they feed, are found by the energetically expensive method of extending the foraging burrows in an apparently random direction until food is encountered. From the burrow pattern, it appears that once a tuber has been located, the neighborhood is then searched thoroughly—seemingly in response to the fact that many tubers reproduce vegetatively and tend to occur in patches. Once located, large items of food such as tubers are left growing and are gradually hollowed out by the mole-rats, small food items are carried to the nest area and eaten there.

The microclimate in all but the very superficial portions of the burrow system is extremely uniform, with humidities (usually) above 90% and temperatures between 30 and 32°C. The mole-rats avoid extreme temperatures in the superficial burrows by restricting their burrowing activities to early morning and late afternoon.

Heterocephalus has a skin that is hairless, except for scattered sinusoidal hairs all over the body; it is well vascularized but lacks sweat glands and the normal mammalian layer of subcutaneous fat (Thigpen, 1940). Consequently, these mole-rats have very high rates of thermal conductance (McNab, 1966). In laboratory studies on single naked mole-rats, McNab (1966, 1968) found them to have a metabolic rate that was less than 40% of that expected, a body temperature of about 32°C, and the poorest capacity for thermoregulation of any known mammal. My own findings confirm these observations (Withers and Jarvis, in preparation). McNab suggests that these modifications reduce the probability of overheating in an environment where evaporative and convective cooling are greatly reduced.

All previous physiological studies on *Heterocephalus* (McNab, 1965, 1966, 1968) have been confined to isolated animals. However, my observations on captive colonies of naked mole-rats have shown them to be highly social rodents. Members of the colony have specific roles in that there are worker and non-worker classes and a dominant breeding female. Furthermore, mutual contact and huddling are important to the mole-rats. I, therefore, suggest that any explanation of their physiology, which does not consider their sociality as well as more aspects of their habitat than just temperature, will at best only give partial answers to the questions raised. This paper attempts to summarize and synthesize our present knowledge of the ecology, physiology, and ethology of these mole-rats and to suggest ways in which these have been influenced by the environmental pressures to which these mole-rats are subjected. More detailed accounts of their social structure and of the physiology of grouped and not single mole-rats will be published later.

MATERIALS AND METHODS

Naked mole-rats were caught by opening a foraging burrow and pushing a spade down behind any animal coming to investigate the damaged burrow. Because of this method, only the worker class of mole-rats were caught. Monthly samples of approximately 30 mole-rats were caught in this way at Mtito Andei, Kenya (240 km southeast of Nairobi), over a complete calendar year. From these animals data on body measurements, reproductive condition, and stomach contents were obtained.

Fifty live mole-rats were collected in the same way at Mtito Andei in early 1974 and established in three "colonies" in the laboratory in Cape Town. After approximately one year each colony had established its social hierarchy and individuals from one colony were marked with subcutaneous injections of india ink, to enable a more detailed study of the social structure of a colony. The two other colonies were used in physiological studies and left undisturbed for breeding.

The preferred ambient temperature range of *Heterocephalus* was determined by establishing a temperature gradient (21°C to 40°C) in a terrarium housing one of the colonies and observing the temperatures selected by single and huddling members of the colony. Observations were made at 10 min intervals and the number of mole-rats sleeping singly or huddled was noted.

Emphasis in the physiological studies was placed on the responses of the mole-rats to a temperature range that approximated the normal burrow temperature. The temperature selection studies, and also field measurements, suggested that the normal burrow temperature lies close to 32°C. McNab (1966) demonstrated that, below 20°C and above about 36°C, *Heterocephalus* almost completely abandons any attempt to thermoregulate—again suggesting that these temperatures lie outside those normally experienced by the mole-rats. For these reasons, my investigations into the effect of temperature on the metabolic rate of *Heterocephalus* were limited to ambient temperatures lying between 20°C and 34°C.

For the metabolic studies, mole-rats were placed in clear perspex containers in a constant temperature chamber. Dried air was drawn through the containers at a known flow rate, which could be varied to suit the experimental temperature and the number of mole-rats in the container. Samples of air were drawn off the air stream and these were analyzed in a Beckman oxygen analyzer OM-1L. The activity of the mole-rats and the chamber temperature was monitored throughout the experiment. At the end of each experiment, the rectal body temperature of each mole-rat was taken using a Bailey Bat-4 laboratory thermometer with attached microprobe. The environmental temperatures used were 20°C, 25°C, 30°C, and 34°C, with the mole-rats in groups of four or singly. The mole-rats were not postabsorptive when placed in the chamber; the emphasis of this study was on determining the responses of mole-rats under as normal a situation as possible. Mole-rats feed intermittently throughout the day and experimental animals were removed from the colony as required. It is highly likely that the animals used in successive experiments were at about the same absorptive stage.

RESULTS

Social Organization

The social structure of the established colony consisted of a single dominant female weighing 53 g, ten mole-rats of both sexes forming the working class and with an average weight of 32 g, and three non-working mole-rats (two males and one female) with an average weight of 38 g. A similar distribution of numbers and sizes appeared to be the pattern in the other two captive colonies.

The dominant female supresses breeding in all the other females in the colony. Before the social hierarchy was completely established in the captive colonies, females coming into estrus at the same time would fight each other, frequently resulting in death for one of them. In the established colonies, this situation never arises and high intensity aggression is never seen. The breeding female is dominant over all other mole-rats in the colony. She initiates courtship and will solicit any male in the colony. However, it is not yet certain whether all males successfully copulate with her. Removal of the dominant female results in another mole-rat assuming the dominant role. This animal appears to come from the non-working mole-rats, but, as is evidenced by the fact that my colonies were established from working class animals, the potential for breeding appears to lie latent in all the females of the colony.

The litter size of mole-rats born in captivity ranged from three to 11 young. Death of a newborn litter may lead to the dominant female breeding again. However, if the young survive, the female appears to breed only once a year. One captive female produced three litters and a total of 24 young within a period of 6 months, only the last litter survived and she has not bred again for 11 months. In the field, breeding appears to be associated with the rainy season (Jarvis, 1969) and it is possible that in unusually good years a litter may be born in both the long and short rains. Growth rates of the young are exceptionally slow, with juveniles taking at least a year to attain adult size (Fig. 1). In spite of their slow maturation rates, the young mole-rats join the worker class at the age of 2 to 3 months.

The non-working mole-rats are the next largest animals in the colony. They remain within the confines of the nest area and are only seen when they emerge to urinate or defecate. Their role in the col-

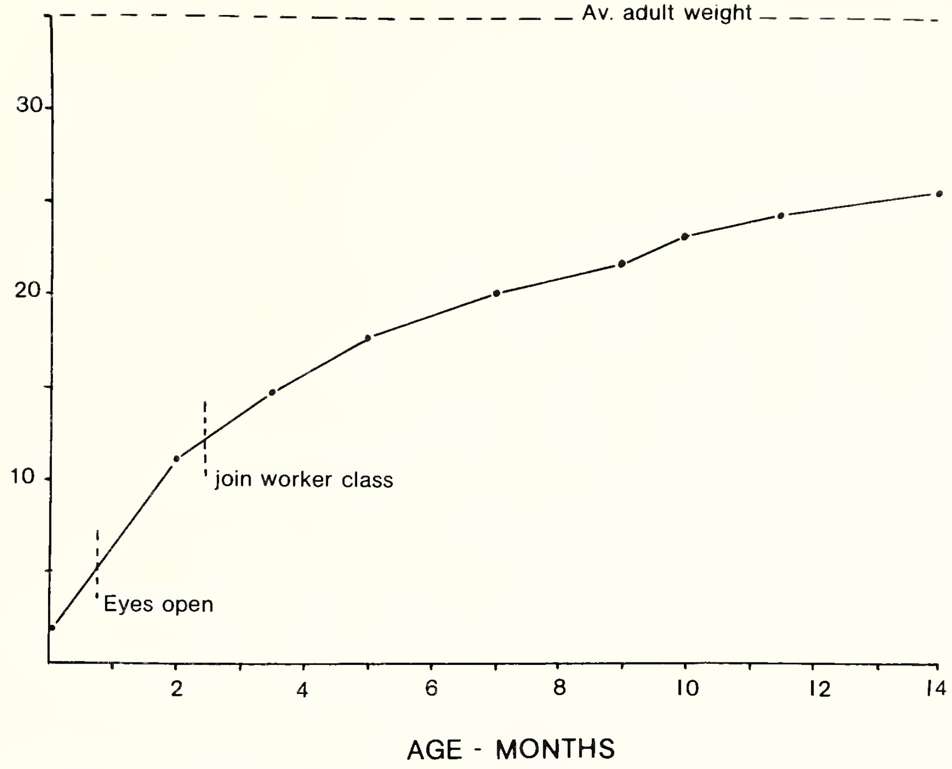

Fig. 1.—The mean growth rate of *Heterocephalus* born and reared in captivity. Compiled from data from two litters (seven mole-rats).

ony appears to be to huddle with the dominant female. It is probable that they are also the most fit to reproduce and that only these males successfully copulate with the dominant female. It is also possible that if the colony numbers are seriously depleted, or if the rains have been exceptionally good, the non-working female(s) may also breed.

The working class mole-rats make up the remainder of the colony, appear to be of an equal sex ratio, and comprise the smallest animals in the colony. The females are non-breeding, but many of the males appear to be potentially capable of breeding in that sperm are produced and they attempt to mount the dominant female when she is in estrus. In the monthly samples collected at Mtito Andei no pregnant or parous females were found in a total of over 150 animals, whereas many of the males had spermatozoa in their vasa deferentia, indicating that the situation found in the captive colony does reflect field conditions.

The working class mole-rats are responsible for the digging of the burrow system, location of the food, transport of food to the non-working animals, and for carrying nest materials to the nest. A high degree of cooperation is shown within this class when they are digging (Jarvis and Sale, 1971). Mutual coprophagy also occurs with the recipient mole-rat (frequently from the non-working class) begging feces from a donor mole-rat.

The smaller size of the working class mole-rats is partly due to the fact that young animals are incorporated into this class at an early age. However, my evidence suggests that the growth rate of these working animals is also retarded. All members of the colony studied were at least 3.5 years old and this size difference was still apparent. Furthermore, the average weight of the whole captive colony is comparable to that of an almost complete colony of 39 mole-rats collected recently at Mtito Andei. These two facts suggest that this size difference is an inherent part of the colony structure.

Another characteristic of the colony is the importance of mutual contact. This appears to be essential for the well-being of the mole-rats and, if forcibly separated from the remainder of the colony, a mole-rat is restless and its overall condition deteriorates. Prior to sleeping, mole-rats frequently seek other members of the colony and, depending

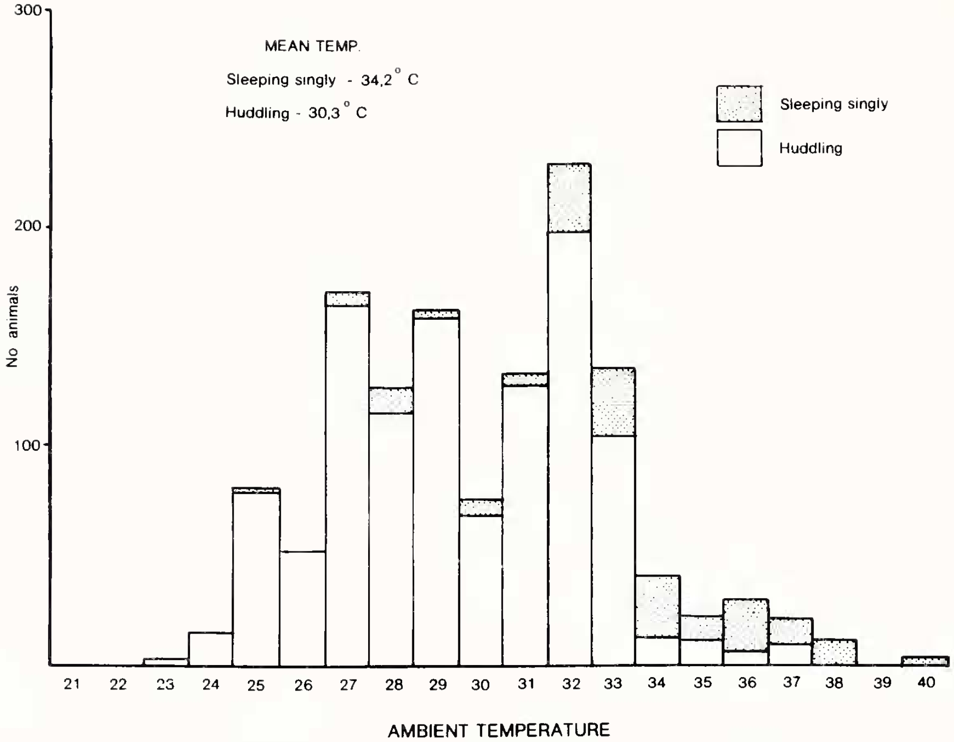

Fig. 2.—Temperature selection in resting *Heterocephalus*. Observations were made at 10-min intervals and the number of animals resting singly or huddled at the different temperatures in the gradient are noted.

on the ambient temperature, either huddle with them or lie close to them. The lower the ambient temperature, the greater the tendency to huddle. This sociality is in marked contrast to the majority of other species of mole-rats, which are solitary aggressive rodents.

It should be stressed here that these observations on the social structure of *Heterocephalus* colonies should, at present, only be regarded as indications of what might be true for the species. More detailed laboratory studies on an almost complete colony of mole-rats captured in October 1977, are at present underway.

Temperature Selection and Metabolic Rates

From the temperature selection studies (Fig. 2), it can be seen that single resting mole-rats generally choose temperatures of between 32 and 38°C with a mean of 34°C. What is not shown in Fig. 2 is the duration of stay at these temperatures. Continuous observations on selected single animals demonstrated that the visits to the higher temperatures tended to be fairly brief and once the mole-rat had "warmed-up" it selected a lower temperature for sleeping. Huddling mole-rats favored temperatures of between 25°C and 33°C in which to sleep (mean 30°C). It can be seen that the temperatures selected by *Heterocephalus* correspond closely to the burrow temperatures of 30°C to 32°C measured in the field. Fig. 2 also clearly demonstrates the strong preference of *Heterocephalus* for huddling rather than solitary sleeping.

From Fig. 3, it can be seen that physiologically, the optimum ambient temperatures also lie close to the normal burrow temperature range. There is a marked reduction in the metabolic rates of mole-rats at 30°C and 34°C and a sharp increase at lower temperatures.

Also apparent from Fig. 3 is that throughout the temperature range studied, there is a significant difference between the metabolic rates of mole-rats resting singly and those huddling. This difference is most marked at 25°C and 30°C where the metabolic rates of the groups of four huddling mole-rats are half of those of the single animals.

At 34°C, the resting metabolic rate of the huddling mole-rats is close to the basal metabolic rate found by McNab (1966) and this temperature falls within the very narrow thermal neutral zone of these mole-rats. McNab (1966) has shown that

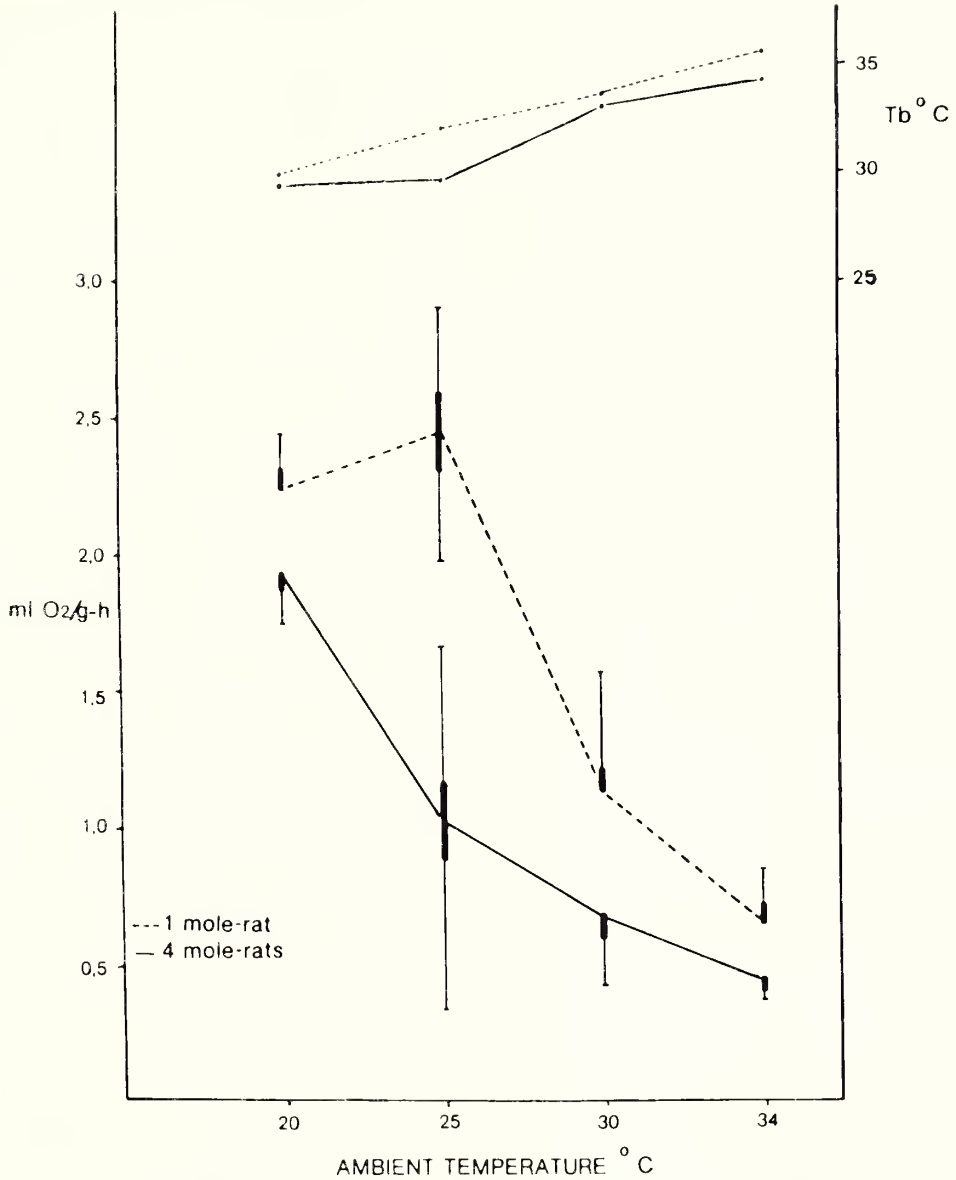

Fig. 3.—The metabolic rates and rectal body temperatures of *Heterocephalus* resting singly or huddling in groups of four, at different ambient temperatures. Standard deviation and standard error are indicated for the metabolic rates. The difference between the metabolic rates of single and huddling mole-rats is significant (P = .001 for 25°C and 30°C; P = .01 for 20°C and 34°C).

above 34°C and below 31°C the energy cost to the animal increases very steeply. My own findings confirm this for the lower temperatures.

The ability of *Heterocephalus* to thermoregulate is limited. The increased oxygen consumption with decreasing temperature and body temperatures elevated above ambient shown in Fig. 3 suggest that although these animals are thermolabile, they show some thermoregulatory ability within the temperature range studied. Outside these temperatures, McNab (1966) found *Heterocephalus* to have a rapidly diminishing ability to thermoregulate.

DISCUSSION AND CONCLUSIONS

The temperature selection studies, environmental measurements, and the narrow ambient temperature range over which *Heterocephalus* appears to thermoregulate and within which oxygen consumption is minimal, all suggest that the naked mole-rat lives in an environment in which temperature fluctuations are minimal. They also suggest that although the burrow temperatures and humidities are fairly high, these mole-rats are rarely exposed to potentially lethal temperatures. Extremes of temperature are only encountered in very superficial burrows and these are avoided by *Heterocephalus* when temperatures are unfavorable. For these reasons, I feel it necessary to look for largely non-thermoregulatory reasons for their unusual physiology and social structure.

I would suggest that food is limiting to *Heterocephalus*. These mole-rats live in semidesert regions where most of their food is in the form of scattered tubers, which, unlike much annual vegetation and grasses, are slow to respond to favorable rainfall. The food supply, although low, is at the same time fairly predictable and it appears that selection in both the physiology and social structure of *Heterocephalus* has favored features, which result in a low but steady demand by the colony.

The colony is so structured that the more expendable mole-rats form the worker class and are involved in the energetically costly search for food. For maximal efficiency these animals do not breed. A limited few of the largest and probably the most genetically fit members of the colony reproduce and remain in the most protected part of the burrow system. These animals are waited on by the other members of the colony and they can therefore channel all their energy into reproduction. They would also huddle with each other and further lower the metabolic cost of living.

For the worker mole-rats, the largest expenditure of energy is in locating the patches of tubers. Once one tuber has been found, the chances of others occurring in the neighborhood are high and the whole area can be exploited with little additional cost to the colony. Evidence from the field suggests that burrowing activities (as indicated by an increased production of mole-hills) are heightened following the rains when the soil is softer and more easily worked than during the dry season. It therefore appears that *Heterocephalus* concentrates its major food finding activities into the most energetically favorable times of the year. The tubers thus located are left growing and exploited as the colony has need of them.

It seems probable that in semidesert areas a colony of mole-rats has a greater chance of surviving than a single animal. In the colony, the cost of burrowing can be shared by the working animals and the chance of locating clumps of tubers enhanced by having more than one animal searching the area. If the colony size is large enough, the search for food can be undertaken on several fronts at the same time. Obviously, there must be an optimum number of worker members to the colony; too many would rapidly exhaust the food found and too few would decrease the chances of finding the food sources.

The burrow systems are extensive and frequently over 100 m long. Distances between tuber patches also appear to be considerable. When a long burrow system has to be dug, a small body size is advantageous in that burrow diameter can be kept to a minimum and the volume of soil displaced and the associated energy cost to the colony kept as low as possible. It is interesting therefore to find that *Heterocephalus* is the smallest of the rodent moles.

Unlike the majority of rodents of similar size, the number of naked mole-rats within the colony appears to remain stable. This is evidenced by the low recruitment rates, limited breeding season, the low growth rates of the young, and the high longevity of the members of the colony (many of my captive animals are at least 5 years old). With this situation, it would appear that at no time of the year would there be a heavy demand on the energy reserves of the colony. Emphasis throughout is on a low but steady demand—a situation well suited to the steady but limited food resources available to the colony. A stable population size also lends itself to the development of a colony where a high degree of social structuring is possible.

McNab (1966) suggests that because of a reduced potential for evaporative and convective cooling in the hot humid burrows in which *Heterocephalus* lives, there may be periods when there is considerable heat storage by the mole-rats, especially when digging. A low metabolic rate and high thermal conductance would reduce the probability of overheating. Although this may well be true, these features may also be linked to their limited energy resources. A metabolic rate that is less than 60% of the expected rate would considerably reduce the daily energy budget of the mole-rats and high rates of thermal conductance open the way to low-cost behavioral thermoregulation.

The possibility that a low metabolic rate is linked to energy conservation was dismissed by McNab because he found that the lower limit of thermoneutrality (31°C) in *Heterocephalus* lay above his mean burrow temperature measurements (30°C). Because of the small size of *Heterocephalus* and their high rates of thermal conductance, this would lead to a marked increase in energy expenditure above the basal level. He argued that if energy conservation was important, there should have been a broad overlap between the burrow temperature and the zone of thermoneutrality.

My measurements of burrow temperatures, during the height of the dry season, gave readings of above 31°C suggesting that, at certain times of the year, burrow temperatures do lie within the zone of thermoneutrality. My studies also suggest that, should the burrow temperature fall, *Heterocephalus* can reduce its rate of thermal conductance, and thus extend its lower limit of thermoneutrality, by huddling. Furthermore, it is possible for *Heterocephalus* to utilize behavioral thermoregulation when temperatures are lower or higher than preferred by simply moving to areas in the burrow system, which have a more favorable temperature. Thus, if heat stressed, the mole-rats could move to deeper and therefore cooler parts of the system where they can off-load heat passively. If too cold, movement to more superficial parts of the burrow during the daylight hours and the early evening would often bring the mole-rat to warmer parts of the system and the animal could again employ passive means to raise its temperature.

Therefore, this evidence suggests to me that here we have a rodent whose physiology, social organization, and behavior have all been influenced by the harsh environment in which it lives—an environment where temperatures are high and food appears to be a limiting factor. An understanding of the ethology and social organization of these mole-rats, and the linking of these with their physiology, suggests that both temperature and food resources must be considered when seeking an explanation for the unique features found in *Heterocephalus*.

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MODELING OF THE POPULATION CYCLES OF TWO RODENTS IN SENEGAL

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ABSTRACT

Models of adaptive strategy to periods of decreasing populations in two rodents in Senegal are given. Actual densities of *Mastomys erythroleucus* and *Taterillus gracilis* are compared mathematically to observed densities. Differences in various ecological parameters of the two species account for their respective adaptive success during periods of low population densities.

INTRODUCTION

The two principal species of rodents—*Mastomys erythroleucus* (Temminck) (Rodentia, Muridae) and *Taterillus gracilis* Thomas (Rodentia, Gerbillidae)—present after the population outbreak of 1975–1976 in the Bandia region of Senegal (14°37′N, 17°01′W), were studied from November 1975 to August 1977. This study particularly involved the large population decrease after the 1975–1976 outbreak. Results are given for the different habitats together—a dry deciduous woodland, some areas of it cut for charcoal production and adjacent areas under cultivation. Different soils are present in Bandia, but all the areas included in this study are on tropical lateritic soils. A further description of the area was presented by Hubert (1977).

METHODS

A large number of animals (more than 1,500 individuals) were caught in snap traps (60 traps during four nights/week in four different habitats) and in 500-m-long lines consisting of 50 live-traps of iron wire (type Manufrance) placed every 10 m. Specimens were autopsied to determine their sexual activity (particularly the number of young in the litter of the females, which varies during the breeding period increasing at first and then decreasing, Table 1). The eye lenses were taken and dried for weighing to determine the age of the individuals collected, by comparison with a diagram established from rodents in captivity (Hubert and Adam, 1975). Thus the approximate dates of birth of each generation are known.

From August 1976, an area of 600 m by 1,000 m was trapped twice each month with 160 traps in rotation and two plots of 4 ha each were trapped every 1.5 months by mark-and-release method, with a 10 m by 10 m grid of 441 live traps of iron wire (type Manufrance). The first trapping allowed determination of the density by CMR method during 10 days. The subsequent trapping (five nights every 1.5 months) allowed the monitoring of the marked population, estimation of the densities, and the distinction between migrations and mortality. Thus a monthly death rate was estimated for different periods; it varied according to the density and to possible epizootic disease being present. The death rate is calculated by the difference between the "load of living animals on the area" at one trapping period and at the following one, that is, the number of the formerly marked animals increased by the newly marked, which will be recaptured later and an average number of "residents" animals representative of the animals crossing the area during the trapping period. This loss could be interpreted as the death rate for a large enough area (where the number of entering rodents is equivalent to the departures) and when the calculation is made with the overall data for different environments taken together. A disease could have occurred from October to December 1976; in fact, a virus ("Bandia" virus, isolated from ticks and one *Mastomys* 10 years ago) was discovered again in January 1977 in four species present in Bandia, after a large population decrease. Its lethal effect has been demonstrated in the laboratory on *Mastomys erythroleucus* by the death of all the young in 10 days. Experiments are in progress for the other species.

A mathematical formula has been adjusted for modeling the population cycle of rodents in terms of the following data, that is, number of young in each litter, mean date of birth of each generation, and monthly death rate for each period. Terms for the formula are as follows: P(t), the population at time t (in days); P_o, the population at time t = o; M, the monthly death rate ($O \leq M \leq 1$); $\bar{n}i$, the average number of young for the i^{th} litter; Ti, the date (in days) of the i^{th} litter. The sex ratio is supposed to be 1.0.

For *Mastomys erythroleucus*, a Hewlett Packard HP 65 computer was employed, using the formula:

$$P(t) = P_0 10^{\frac{t}{30}\log(1\text{-}M)} + \frac{P_0\bar{n}_1}{2} 10^{\frac{T_1}{30}\log(1\text{-}M)} \cdot 10^{\frac{t\text{-}T_1}{30}\log(1\text{-}M)}$$

$$+ \frac{P_0\bar{n}_2}{2} 10^{\frac{T_2}{30}\log(1\text{-}M)} \cdot 10^{\frac{t\text{-}T_2}{30}\log(1\text{-}M)}$$

$$+ \frac{P_0\bar{n}_3}{2} 10^{\frac{T_3}{30}\log(1\text{-}M)} \cdot 10^{\frac{t\text{-}T_3}{30}\log(1\text{-}M)}$$

$$+ \frac{\bar{n}_4}{2}\left[P_0 10^{\frac{T_4}{30}\log(1\text{-}M)} + \frac{P_0\bar{n}_1}{2} 10^{\frac{T_4\text{-}T_1}{30}\log(1\text{-}M)}\right] \cdot 10^{\frac{t\text{-}T_4}{30}\log(1\text{-}M)}$$

The formula is not simplified, as it was used for the programming of the HP 65. The evolution of the different generations is given by the same program, where $\bar{n}_2 = \bar{n}_3 = \bar{n}_4 = 0$, and so on.

For *Taterillus gracilis*, it is not possible to use the same program because too many generations occur in the same year (nine from August 1975 to August 1976). In this case we used the following formula (example from May 1975 to August 1976):

$$P(t) = P_0F + \frac{\bar{n}_1}{2} P_{06}F + \frac{\bar{n}_2}{2}(P_{06} + P_{03})\,F + \frac{\bar{n}_3}{2} P_0F$$

$$+ \frac{\bar{n}_4}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right)\cdot F + \frac{\bar{n}_5}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right)\cdot F$$

$$+ \frac{\bar{n}_6}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right)\cdot F + \frac{\bar{n}_7}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right)\cdot F$$

$$+ \frac{\bar{n}_8}{2}\left[P_0 + \frac{\bar{n}_1}{2} P_{06} + \frac{\bar{n}_2}{2}(P_{06} + P_{03})\right]\cdot F$$

$$+ \frac{\bar{n}_9}{2}\left[P_0 + \frac{\bar{n}_1}{2} P + \frac{\bar{n}_2}{2}(P_{06} + P_{03}) + \frac{\bar{n}_3}{2} P_0\right]\cdot F$$

$$+ \frac{\bar{n}_{10}}{2}\left[P_0 + \frac{\bar{n}_1}{2} P_{06} + \frac{\bar{n}_2}{2}(P_{06} + P_{03})\right.$$

$$+ \frac{\bar{n}_3}{2} P_0 + \frac{\bar{n}_4}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right) + \frac{\bar{n}_5}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right)$$

$$\left. + \frac{\bar{n}_6}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right) + \frac{\bar{n}_7}{2}\left(P_0 + \frac{\bar{n}_1}{2} P_{06}\right)\right]\cdot F$$

$$\text{where: } F = 10^{\frac{t}{30}\log(1\text{-}M)}$$

Table 1.—*The main reproductive data for* Mastomys erythroleucus *and* Taterillus gracilis *in the Bandia area during the 1975–1976 and the 1976–1977 breeding periods.*

Species	Approximate date of each generation	Average number of young per litter	Participation of young animals in breeding
Mastomys erythroleucus	1 November 1975	8	–
	1 December 1975	13	–
	12 January 1976	13	–
	28 February 1976	10	+
	1 October 1976	8	–
	1 November 1976	10	–
	1 December 1976	13	–
Taterillus gracilis	10 May 1975	3	–
	20 August 1975	3	–
	15 September 1975	4	–
	1 November 1975	4	–
	5 December 1975	5	–
	30 December 1975	5	–
	25 January 1976	5	–
	25 February 1976	3	–
	25 March 1976	3	–
	5 May 1976	1	+
	20 August 1976	3	–
	25 September 1976	4	–
	25 October 1976	5	–
	25 November 1976	5	–
	20 December 1976	5	–
	20 January 1977	5	–
	30 March 1977	3	+

P_{06} is the number of animals older than 6 months in P_0; P_{03} is the number of animals between 3 and 6 months old in P_0. We know $P(464) = 6$; a sample of *Taterillus* caught at $t = o$ gave the population structure (dry crystalline lens weight), so we know also $P_{06} = f(P_0)$ and $P_{03} = f(P_0)$ and now we can compute P_0; P_0 known, we can compute $P(t)$ from $t = 0$ to 464 days. The observed density (by CMR method) of August 1976 is used as the basis of all the calculation for the two species.

RESULTS

The two graphs (Figs. 1 and 2) present the following data: The total fluctuations in the number of animals present per hectare at time t; the trapping population at time t, consisting of adults and recently weaned young; the appearance and growth of each litter until the disappearance of all its individuals; the ratio of each age group in the population at time t.

It is easy to see that if the actual densities of the two populations are now equivalent and close to the observed densities, they did not have the same previous development.

Mastomys erythroleucus accounted for a large portion of the population outbreak of 1975–1976, and its densities were very high during the last year. The possible occurrence of an epizootic disease (or

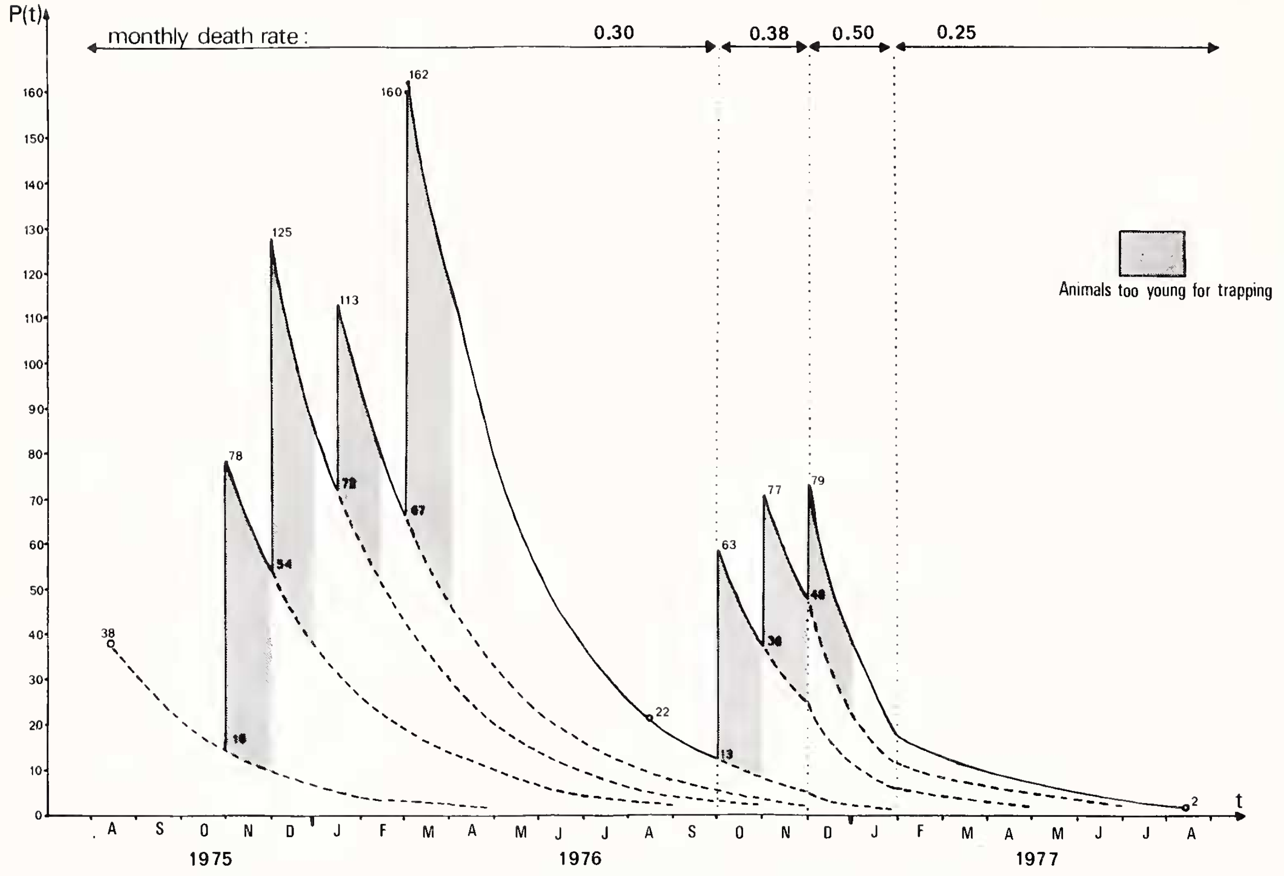

Fig. 1.—Fluctuations in the population level of *Mastomys erythroleucus* on 1 ha near Bandia, Senegal.

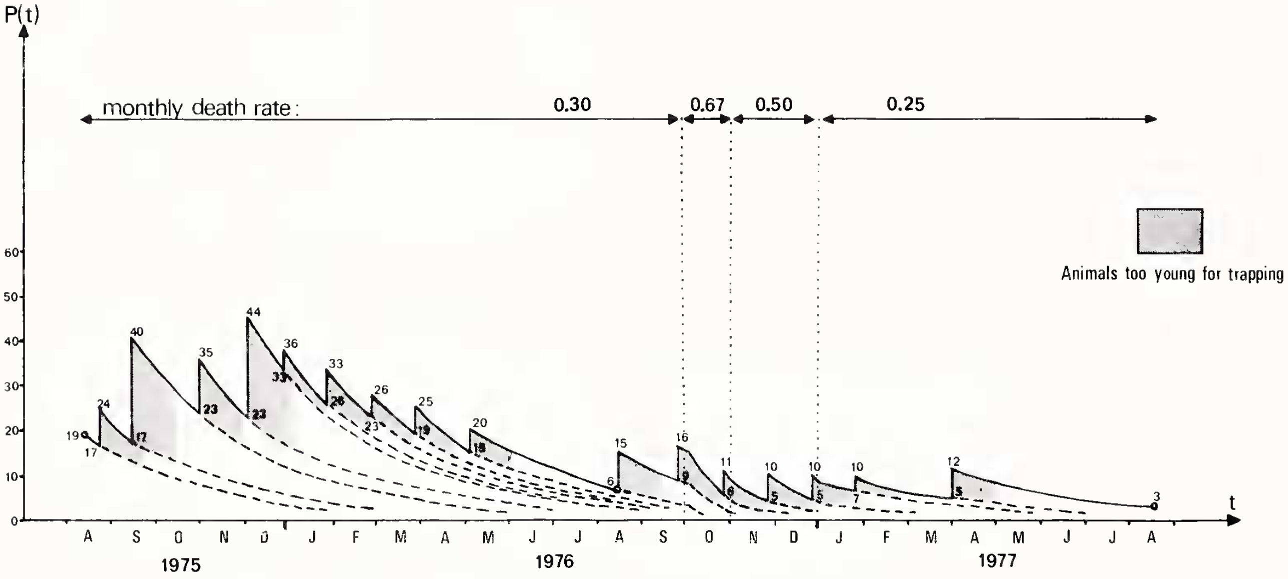

Fig. 2.—Fluctuations in the population level of *Taterillus gracilis* on 1 ha near Bandia, Senegal.

a different factor increasing the death rate) reduced the population considerably to the actual rate in spite of large reproduction. Mortality of the adults was high, and that of the young was such that the first litters, which had bred at the end of the breeding period in 1975–1976, could not do so in 1976–1977.

Although the densities of *Taterillus gracilis* were relatively high in 1975–1976, there was no population outbreak of this species. Densities were almost unchanged and less subject to variations during that year because of a longer breeding period and a higher individual survival rate. However, the *Taterillus* population was also affected by the disease, as the monthly death rate increased considerably and the population remained in the fields only because of the continuation of the breeding period late in the year.

DISCUSSION

Once more the difference of adaptative strategy appeared between *Mastomys* and *Taterillus* populations as discussed below.

Mastomys erythroleucus.—This species has a short breeding period, but with large litters (eight to 13 young per litter), allowing the population to reach a very high level. This large production of young animals permits colonization of new environments, as described by Hubert (1977). They also possess resistance to various disasters (drought, diseases) and the ability to exploit the environment when the production of young is highest, as in the beginning of the dry season. These young animals supply the parental generation for the next year.

Taterillus gracilis.—The breeding period of this species continues for a longer time; it begins earlier in the wet season and continues later into the dry season, with the largest participation of the young animals. The fertility rate is lower than in *Mastomys*; three to five young are produced per litter according to the period of the breeding season. Populations are more regularly present in the fields than those of *Mastomys* and they resisted the disease by maintaining an almost standard breeding period in 1976–1977. The individuals of this species that live more than one year are more numerous than in *Mastomys,* thereby maintaining the population in large areas.

For this computation, the death rate was supposed to be constant throughout the life of the animals, and all the females older than 6 months, or 3 months if the young females do participate to the breeding period, are supposed to be littering at each generation. These two hypotheses do not contradict the observed data. Using observed densities in August 1976 as the basis of calculation, the expected densities obtained for August 1977 are very close to the observed ones for the same period (that is, about two individuals per ha for each species).

The resemblance between observed and computed data allows us to do the same calculations on the fluctuations of the densities. This model can also be used for the calculation of productivity by estimating the complete number of rodents produced, including the juveniles too young to be trapped.

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RADIO-TRACKING OF A SMALL RODENT, *HYBOMYS UNIVITTATUS*, IN AN AFRICAN EQUATORIAL FOREST

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ABSTRACT

Preliminary studies of home range, activity periods, and movement in *Hybomys univittatus* (Mammalia: Muridae) was studied by using radio-tracking. Comparisons between males and females indicate males have larger home ranges and are generally more restricted to them than females. Both sexes are diurnal in their periods of activity but females are less active than males.

INTRODUCTION

Most small rodents are easily caught in live-traps. However, it is often difficult to watch them in the field, especially in closed biotopes. Therefore, since 1975, I have used a radio-tracking technique (transmitter AVM, SM1 type; telemetry receiver model LA 12, with Yagi antenna).

I have been working for two years in the Central African Empire, near M'Baiki. These preliminary results concern a diurnal murid, *Hybomys univittatus* (Peters, 1876).

This mouse measures 100 mm in length of head and body and weighs 50 to 70 g. The fur is soft. The dorsal color ranges from light yellowish brown to dark brown, with a black middorsal stripe that extends from the nape to the base of the tail. The ventral color ranges from tawny to grayish white.

This rodent species is only terrestrial. It lives in burrows in which it builds nests made of twigs. An individual may have three or four burrows but one is more often occupied than the others. *Hybomys* is solitary in its burrows.

METHODS

Experimentation

Ten *Hybomys*, six males and four females of various ages, have been observed by the radio-tracking technique during December 1975, January, April, and May 1976, and January, February, April, and May 1977; that is to say in the dry season and and the beginning of the rainy season.

During these observations, one female aborted its young; two animals, male and female, lost their transmitters (the female was just leaving its home range); finally, a male died of a wound made by the antenna-collar that it had been carrying for 3 weeks. The transmitter weighs 12 g with its wrapping.

Environment

These observations were made in a dense equatorial forest in the process of secondary seral stage. There the underwood is dense and the ground is covered with branches and trunks of dead trees intermixed with creepers.

An area of 10,000 square m has been gridded with narrow cross-trails at 20-m intervals, to compensate for the weak range of the transmitters. These cross-trails have been just roughly cleared, to reduce reluctance in the rodents to cross them. At each crossing a Sherman trap or a Saint-Etienne trap was placed. The rodents caught by this method have been marked by toe-clipping and thus it has been possible to watch them year round. The most assiduous visitors to the live-traps were selected to carry a transmitter; this selection increases the chance of recovering the instrument later.

RESULTS AND DISCUSSION

Home Range of Hybomys

Captures and recaptures gave us information about the home range of *Hybomys*. From radio-tracking, it has been possible to delimit the areas more exactly. They vary from 4,500 to 6,100 square m for the cases of males and from 1,400 to 1,800 square m for females.

A male spends its entire adult life (about 12 months) in the same home range. When the individual dies, its home range remains vacant for a while, but within a few weeks or months, another male or a female will take possession of the area. The limits of the new individual's home range will not be exactly the same as those of the previous one, particularly if the new individual is a female.

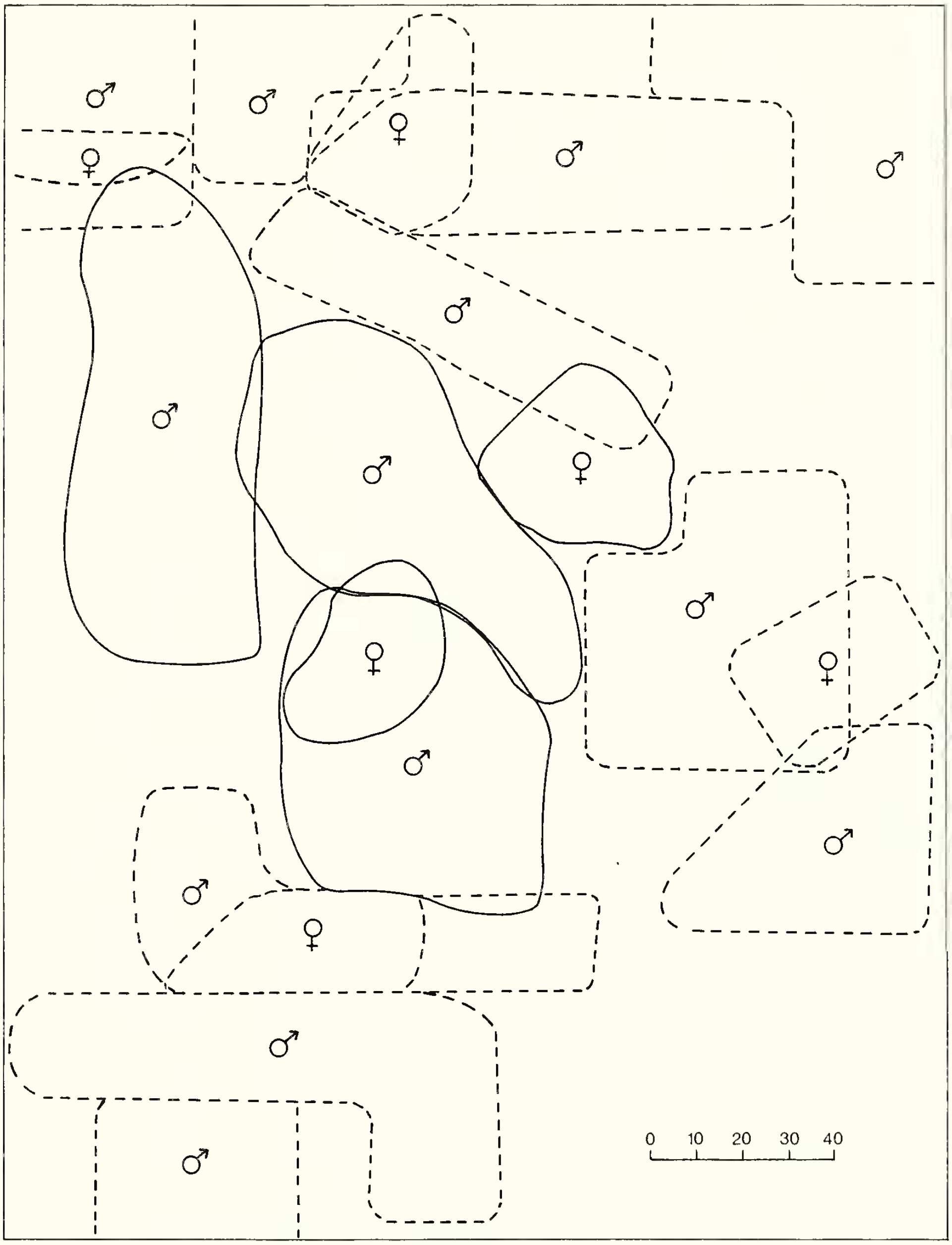

Fig. 1.—Home ranges (in meters) of male and female *Hybomys univittatus* from January to May 1976. Four home ranges were calculated from results of the radio-tracking technique. Broken lines indicate the home ranges defined by the "capture-mark-and-release" technique.

The home ranges of neighboring males do not overlap. If one of the males dies, its neighbor can enlarge its own home range but this enlargement is always moderated. Only the young *Hybomys* can move from one home range to another, contributing to the species dispersal. For instance, a young female left its home range and lost its transmitter at 280 m from its burrow. This distance represents seven times the width of its home range. The animal certainly went farther than that because we never caught it again.

Males do not tolerate other males in their home range. If two males come together, the owner gives chase to the other individual and bites it cruelly if owner overtakes the intruder. Some males share their home range with one or two females, which occupy smaller areas (see Fig. 1). It might happen that the female who lives with a male during some

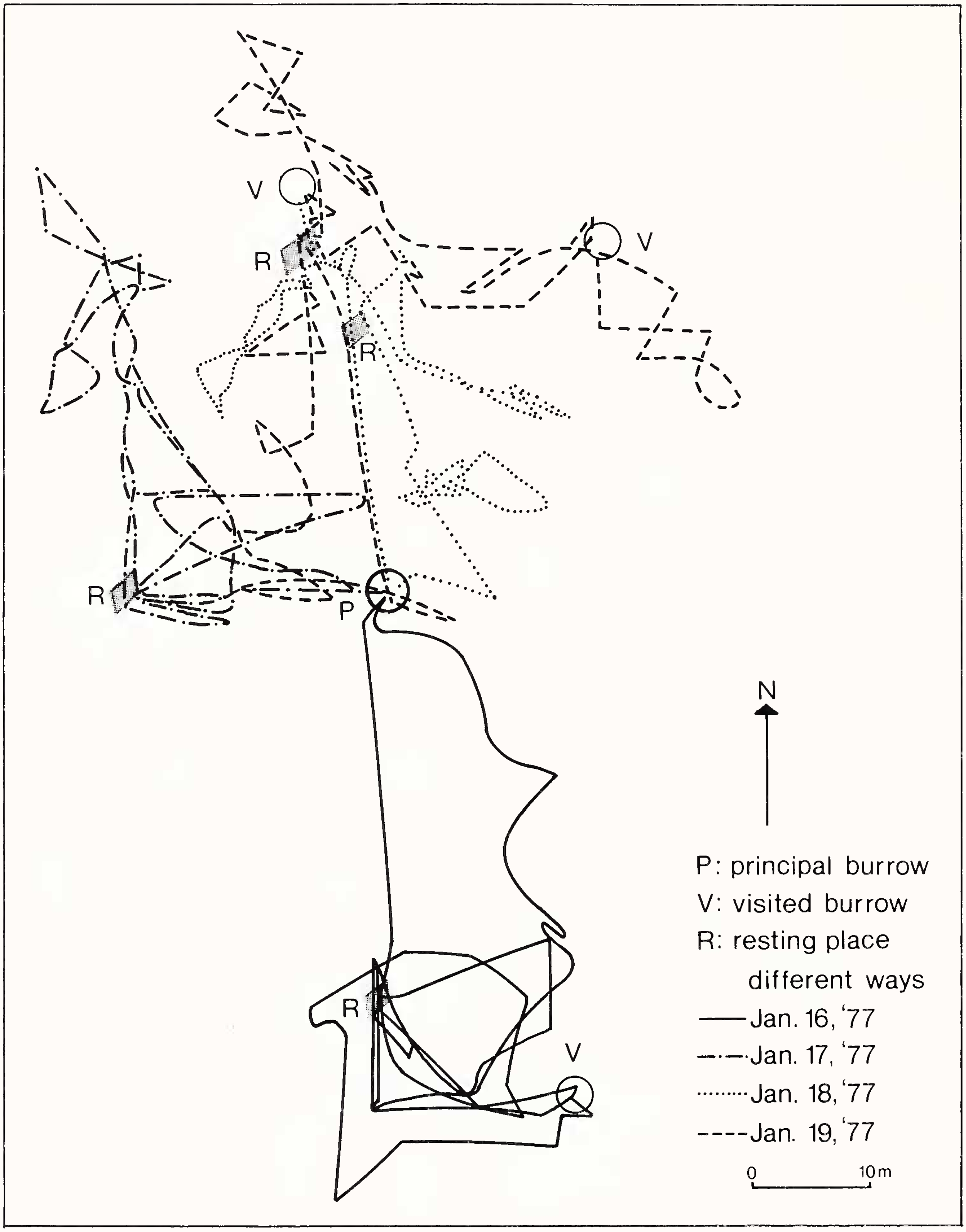

Fig. 2.—Movements of an individual male *Hybomys* monitored by the radio-tracking technique. Daily movements are recorded for 4 days in January 1977.

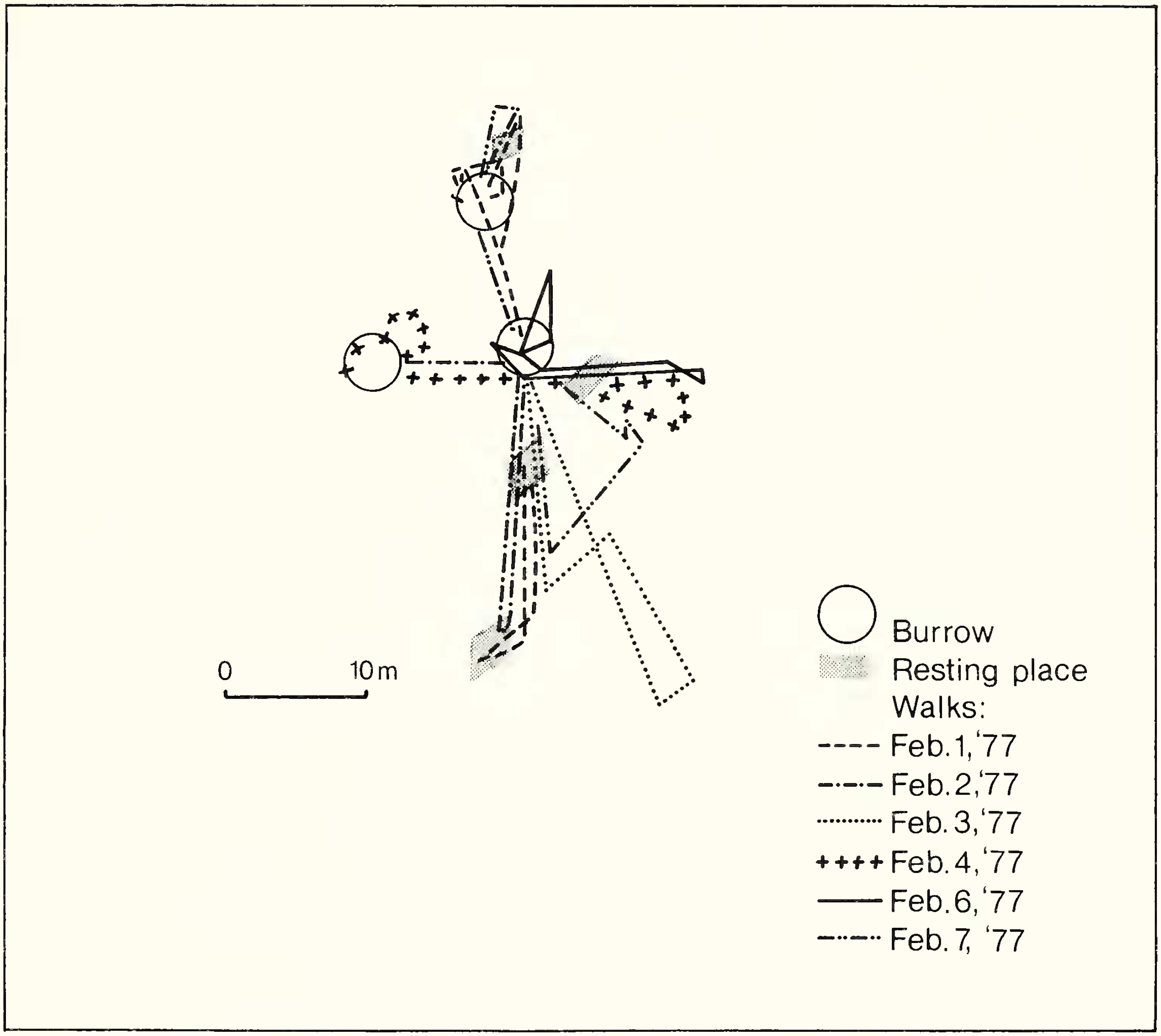

Fig. 3.—Movements of an individual female *Hybomys* monitored over a 6-day period in February 1977. Numerous short movements around the burrows are not indicated.

months chooses to go with a neighboring male. However, it can be seen that the coexistence of the two sexes is not the rule. The individuals do not sleep in the same burrow. Surely the overlapping of the home ranges favors mating in the breeding season.

Hybomys *Activity in the Forest*

All the activity of *Hybomys* outside of the burrow is diurnal. Males and females do not have the same type of activity.

Case of males.—The activity timetable of males is rather regular for an individual but it varies from one individual to another. Thus an early-rising male may leave its burrow near 7:20 A.M., whereas another may wait until 8:30 to 8:50 A.M. The individual will run quickly a distance of 20 to 30 m to reach a part of its home range that it will be exploring carefully during the next several hours. It follows a different path each day and some of them do not visit the same part of their home range on two consecutive days (see Fig. 2).

In the morning, movement is done at top speed, but in the afternoon the animals are not so swift. During the day, we have observed short periods of decrease in movement, but they are not a true rest period, because the animal feeds or performs its toilet.

Besides these short periods of non-movement, there are two resting periods, one or two h long. The first is in the middle of the morning and the second in the course of the afternoon (for instance between 9:00 and 10:00 A.M. and between 4:30 and 5:30 P.M.). Males take their rest in their principal burrow (that is to say in the burrow where the animal spends most of its nights) or in some special areas that *Hybomys* like very much (for example, piles of twigs, dead branches, underpart of a blown down trunk, or old "termite houses" with many holes). Sometimes several species of rodents share the same "termiterium." *Hybomys* returns to these places many times in the course of its walks.

Each day, a male covers a distance of about 500 m. This distance has been evaluated by summing up all the recorded movements. I have not been able to take into account the numerous sporadic movements and small bolts that the animal does in quest of food; such activity is not perceptible with my method of telemetry.

The mean speed of a male *Hybomys* varies between 110 cm/min in the morning, to 80–90 cm/min in the afternoon, but it can reach a higher speed. For instance, an animal released at dusk at the place of its capture tries only to return to its resting place and it does that at a speed of 720 cm/min. It does not run directly to its burrow, but describes a large circle, as if trying to get its bearing, and it does not come into its hole without turning around first.

A male usually spends the nights in the same burrow. It regularly visits three or four other burrows in which it occasionally sleeps, and sometimes visits the burrow of a female, which may live in an overlapping home range.

The last return to the principal burrow takes place between 6:00 P.M. and 6:05 P.M. or between 5:45 and 5:50 P.M., according to the individuals involved. If the males don't begin their activity at the dawn, they cease their activity at full dark in the forest.

Female activity.—Females are not as active as males. They move only short distances; they circle their burrows, entering into them often, even if there are no young in the nest. They repeat this frequently and do not go further than 50 m from their burrows. Thus, females are sedentary, but, quite curiously, they have several burrows and can spend a night in each of them; those burrows are about 10 m apart (Fig. 3).

In the course of a day, a female can spend long periods out of its burrow. It remains motionless under dead leaves, and returns to the same places for consecutive days between 10:00 A.M. and 4:00 P.M. At times, it takes a long rest in its burrow, for 40 min to 2 h between 10:00 A.M. and 4:00 P.M.

Female activity begins between 7:45 and 8:30 A.M. and the activity ceases between 5:00 and 6:00 P.M.

The time of activity of a female and of a male are not very different, but the females are not so regular. The most striking difference between male and female activity concerns the intensity of this activity and the length of the movement. It appears that females are not so strongly attached to their home range as males, since even as adults, they can leave one home range for another. A female, which lived in January on a part of the home range of a male, was caught in April, and watched during 3 weeks by the radio-tracking technique on another area. This latter was situated 70 m from the first area, overlapping the home range of another male slightly (see Fig. 1). In addition, females are not so "home-loving" since they scarcely spend two consecutive nights in the same burrow when they have no young.

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SEASONAL POPULATION CHANGES IN RODENTS IN THE KENYA RIFT VALLEY

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ABSTRACT

Live trapping of small rodents was undertaken on three grids each of 81 traps in grassland and scrub vegetation in the middle of the wet and dry seasons in Nakuru National Park, Kenya. Snap trapping was carried out concurrently. The most abundant species was *Arvicanthis niloticus; Praomys natalensis, Lemniscomys striatus, Otomys angoniensis,* and *Rhabdomys pumilio* were obtained in moderate number. There were relatively greater changes in densities in the grassland than in the scrub at the two trapping occasions; densities were invariably highest in the dry season. Reproduction was maximal in the wet season and had terminated by the dry season. Populations of *Arvicanthis* contained animals of all ages at both periods, whereas *Praomys* had a much broader age spread in the wet than the dry season when few older animals were present. The scrub vegetation apparently forms population reservoirs at adverse times of the year when it appears that the grassland is unable to provide suitable conditions.

INTRODUCTION

In recent years several studies have been undertaken on the ecology of small rodents in the grasslands of East Africa (Delany 1964, Delany and Neal, 1969; Neal, 1970; Cheeseman, 1975; Taylor and Green, 1976). With the exception of Taylor and Green's (1976) work, which was undertaken in the same region as the present study, the remaining research has been carried out in western Uganda. These latter studies examined times of breeding, population dynamics, and other aspects of the ecology of animals in areas where there are typically two discrete rainy seasons. In Uganda it was found that the breeding of most species of small rodents commenced soon after the onset of the wet season and terminated shortly after it ended (Delany and Neal, 1969). Inevitably, these breeding patterns exerted their influence on population dynamics throughout the year (Cheeseman, 1975).

In their study at Nakuru and Kitale in Kenya, Taylor and Green (1976) examined the relations between reproduction, diet, and climate. They demonstrated that the seasonal effects of rainfall on the vegetation brought about variations in the quality and quantity of available food for rodents, some of which could be associated with the regulation of breeding. This valuable work was based upon animals obtained by snap trapping and did not provide detailed information on seasonal changes in population densities and structure. The present study supplemented and extended the work of Taylor and Green (1976) by providing information on these aspects of small rodent ecology in a typically grassland locality having a single protracted rainy season. This rainfall pattern prevails in many parts of the Kenya Rift Valley. Here the rains build up to a peak in March and April from the dry season in December and January. Typically, they continue into November without a break (Fig. 1). This attenuated wet season is not commonly found in the seasonal tropics where the rains usually last for appreciably shorter periods. The field work in this study was undertaken at Baharini Wildlife Sanctuary of Nakuru National Park on the northern shores of Lake Nakuru, Kenya, during July, August, and December 1974 and January 1975. These periods coincided with the middle of the wet and dry seasons.

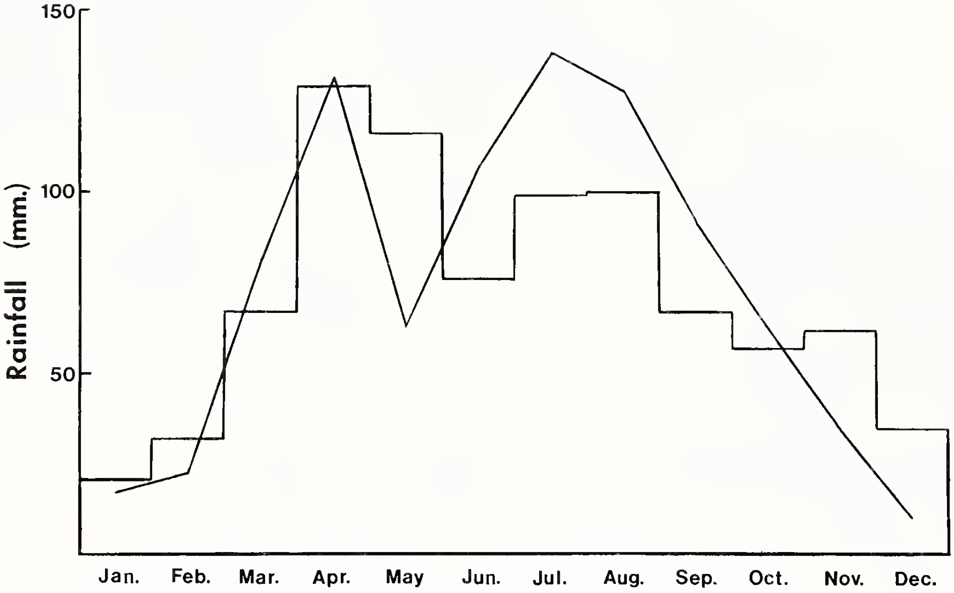

Fig. 1.—Rainfall figures at Nakuru Railway Station. The histograms represent the mean figures from 1904 to 1970 and the continuous line 1974 figures (source: East African Meteorological Department).

STUDY AREA

The field research was undertaken in a relatively small area of grassland with occasional scrub to the north of Lake Nakuru and never more than 3 km from the lake shore. Hereabouts the lake is fringed by a narrow strip of olive bark acacia (*Acacia xanthophloea* Benth.) woodland with an understory of shrubs, herbs, and grasses including *Setaria pallidifusca* (Schumach) C. E. Hubb, *Erlangea cordifolia* (Benth. ex Oliv.), *Tagetes minuta* L., *Abutilon mauritianum* (Jacq.) Medic., and *Solanum* sp. Beyond this woodland lies an extensive and level area of grassland, which to the east rises to a stony hillside covered by small *Acacia* trees. Here extensive rock outcrops result in a poor covering of ground vegetation.

Between the lakeside woods and the hillside, the extensive grasslands were interspersed with very small patches of scrub, and the occasional tree or small clump of trees. It was within an area approximately 3 km square of this grassland and scrub that the research was concentrated. This was at an altitude of 1,870 to 1,950 m above sea level. Within this area live trapping was undertaken in five grids and snap trapping over the area as a whole within its typical vegetation types. As considerable reference is subsequently made to the grid trappings, their vegetation is given in some detail.

Grids 1 and 2 were placed in an extensive and typical area of grassland. Here in July much of the vegetation was 1 m or more tall and consisted mainly of *Hyparrhenia hirta* (L.) Slapf., *Themeda triandra* Forsk. and *Chloris gayana* Kunth. *Sporobolus pyramidalis* Beauv., *Setaria pallidifusca* (Schumach) C. E. Hubb, *Aristida adoensis* Hochst., and *Harpachne schimperi* A. Rich. were also present. The area was interspersed with a few small *Acacia* trees, the occasional compact bush of *Lippia javanica* (Burm. f.) Spreng, small woody *Hibiscus aponeurus* Sprague and Hutch., and scattered *Solanum* plants up to approximately 60 cm tall. There were numerous small herbs adding to the thickness of the ground cover. Over most of these grids the grass and herbage formed a dense cover although there were a few small areas of sparsely covered ground. In addition to the rodents obtained in this work, other mammals present included spring hares, *Pedetes capensis* (Forster), mole rats, *Tachyoryctes splendens* (Ruppell), ant bears, *Orycteropus afer* (Pallas), and steinbok, *Rhaphicercus campestris* (Thunberg). A herd of waterbuck, *Kobus ellipsiprymnus* (Ogilby), were occasional visitors.

Grid 3 contained slightly different vegetation to grids 1 and 2. Although there was a good grass cover of *Hyparrhenia*, *Themeda*, *Setaria*, *Aristida*, and *Chloris* on about three quarters of the grid, more herbs and shrubs interspersed with the grasses over the remainder. These included *Erlangea, Lippia, Indigofera vohemarensis* Baill., *Leonotis*, and *Tagetes*. There was also a small clump of trees.

The vegetational character of grid 4 and grid 5 was quite different from the preceding three grids. In view of the detailed studies undertaken on them, these two grids had their vegetation mapped. Whereas grids 1 to 3 were within grass-dominated vegetation, 4 and 5 had a much more shrub and bush character. On grid 4 grasses (*Hyparrhenia, Themeda, Aristida, Chloris*) were present but covered little ground. *Lippia* was abundant and dense, attaining a stature of 50 to 150 cm over much of the grid. It was frequently accompanied by dense *Cynodon aethiopicus* Clayton and Harlan. Among the other plants present were *Ocimum suave* Willd., *Alternanthera aspersa, Zehneria scabra* (L. f.) Sand., *Bidens pilosa* L., *Rumex usambarensis* (Dammer), *Tagetes, Leonotis, Solanum*, and *Erlangea*. Over much of this grid the thickness of the vegetation made it difficult to penetrate and necessitated the establishment of narrow footpaths.

Grid 5 was similar to grid 4 in that it had the same shrubby character and contained large amounts of *Lippia*. There was more grass in grid 5 although the shrub-like character was much in evidence. It did not contain as great a variety of herbs and woody plants as grid 4 and was more readily penetrable. Grids 4 and 5 were located 2 km from the track around the lake along the road to Lanet. They were situated 5 m to the west of this road and almost parallel to it. The two grids had the same compass bearings and were only 21 m apart. Because of their spatial relationship to the road, it was not possible to align them so that they had a continuous base line. Grid 5 was therefore displaced 10 m west of grid 4. These grids covered 40 square m. The vegetation described for these grids was largely confined to the two small patches encompassed by them. They were surrounded by the grassland described for grids 1 and 2.

The vegetation described in these 5 grids is typical of the non-wooded areas to the north of Lake Nakuru. The removal trapping was undertaken in these types of vegetation. Neither cattle grazing nor burning had taken place in the area for some years prior to this study.

In 1974, the rainfall at Nakuru (Fig. 1) was similar to, if not quite the same as, the statistical average pattern. Higher than average rains fell from May to September and the mid wet season trough was earer than usual. However, April had its typically high rainfall and the total figure for 1974 of 887 mm was only 26 mm more than the mean. It would therefore appear that the figures for 1974 approached the typical situation.

METHODS

Grid trapping was undertaken using 81 (9 by 9) of the larger Sherman live traps. On grids 1 and 3 the spacing was 10 m, on grid 2, 20 m with alternate trap sites of grid 1 forming the central core of this grid, and on grids 4 and 5, 5 m. Traps were examined twice daily in early morning and late afternoon. On capture, each animal was identified to species, weighed, sexed, marked by toe clipping, and the location of the trap in which it was caught recorded. For males it was noted if the testes were descended and for females if they could be recognized as pregnant and/or lactating. They were then released. Traps were set on the grids on the following dates: grid 1—11–14 July 1974, 3–8 January 1975; grid 2—15–17 July 1974; grid 3—1–3 August 1974; grid 4—5–11 August 1974, 28 December 1974 to 2 January 1975; grid 5—18–24 August 1974, 20–25 December 1974. To ascertain occupancy immediately peripheral to grid 4 at the August trapping two rows of traps 5 m apart were set along the two sides of this grid that were not bounded by the road or grid 5. They were in grassland and were set from 14 to 16 August 1974. The catch was handled in the same way as other live trappings.

Snap trapping took place concurrently with the live trapping using 40 commercially produced rat traps. They were set in trap lines and moved at irregular intervals largely in response to their success. The animals caught by these traps provided more detailed information on reproduction and relative age than the live caught animals. They had the standard external measurements taken and were weighed. Reproductive and development conditions were recorded. These included the condition of the uterus (active, distended, inactive, undeveloped, number of placental scars), number of embryos, weight of reproductive tract of pregnant females, lactation, descent and size of testes, and juvenile pelage. Relative ageing was undertaken using seven categories of dental attrition in the upper molar row. The categories, erected for this study, ranged from the incompletely erupted row of Class I to the row displaying considerable dentine exposure in Class VII. A similar method was used by Delany (1971) and Cheeseman (1975). Throughout all the trappings a banana-flour paste was used as bait.

RESULTS

Numbers Caught

In grids 1, 4, and 5 (Table 1), there was a considerable increase in rodent numbers between July and August and December and January. These increases ranged from double to fifty-fold in the case of grid 1. *Arvicanthis* and *Praomys* comprised just

Table 1.—*Numbers of rodents caught on grids 1, 4 and 5.*

	Grid 1				Grid 4				Grid 5			
	July		January		August		December		August		December	
Species	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Arvicanthis niloticus (Desmarest)	0	0	20	20	4	13	25	25	22	13	31	25
Dendromus melanotis Smith	0	0	0	1	0	0	0	0	0	0	0	0
Lemniscomys striatus (L.)	0	0	0	0	3	0	4	8	0	0	0	0
Otomys angoniensis Wroughton	0	0	0	1	2	1	0	1	2	0	3	2
Praomys natalensis (Smith)	0	1	1	0	13	7	16	7	3	3	7	6
Rhabdomys pumilio (Sparrman)	0	0	6	3	0	0	7	7	0	0	9	2
Total	1		52		43		100		43		85	

over 80% of the catch. The patterns of increase from mid-wet to mid-dry season were not the same for each grid. On all three grids there was a considerable increase in the numbers of *Arvicanthis* and *Rhabdomys* while on grid 4 *Lemniscomys* and grid 5 *Praomys* also showed appreciable increases. On grid 4, three *Arvicanthis*, three *Praomys*, and one *Rhabdomys* caught in August were recaptured in December; on grid 5 the comparable figures were six *Arvicanthis* and one *Praomys*. These figures suggest either a low survival or appreciable immigration from the grids. At each trapping period there were a small number of animals caught on both grids. In August there were four *Arvicanthis* and in December-January seven *Praomys*. This indication of relatively small home ranges obtains support from catches from the two peripheral lines of traps by grid 4 in August. One *Arvicanthis*, five *Praomys*, and one *Otomys* were trapped. Of these, only one *Praomys* had been caught on the grid in one of the outer rows of traps.

The catches on grids 2 and 3 were small and they were not worked in the dry season. No animals were taken on grid 2 and one *Mus minutoides* Smith and two *Lemniscomys striatus* were obtained from grid 3.

The animals caught by snap trapping are given in Table 2. Similar trends are witnessed in species abundance as were found for the live trapping with *Arvicanthis* and *Praomys* most frequently caught. Two additional species (*Lophuromys* and *Aethomys*) were obtained by these trappings.

Population Densities

Fleming's (1971) direct enumeration method has been used to obtain population densities. This is likely to be a conservative estimate as it assumes that all the animals inhabiting the grid are caught in the course of trapping. To provide an estimate of the catchment area of the grid a strip with a width equivalent to the average distance (Av.D.) between successive captures is added to the trapped area. This estimate varies from species to species, from grid to grid and from one time to another. The summary of calculable estimates is given in Table 3. Av.D. could not be obtained for those species where few recaptures were made. The available data suggest that in grids 4 and 5, when allowance

Table 2.—*Rodents obtained by snap trapping.*

	July/August		December/January		
Species	♂	♀	♂	♀	Total
Aethomys chrysophilus de Winton	0	0	0	1	1
Arvicanthis niloticus	16	12	26	26	80
Dendromus melanotis	0	0	0	1	1
Lemniscomys striatus	3	0	1	1	5
Lophuromys flavopunctatus Thomas	0	0	1	1	2
Otomys angoniensis	5	1	3	2	11
Praomys natalensis	12	16	11	9	48
Rhabdomys pumilio	0	1	7	4	12

Table 3.—*Estimates of population densities.*

Grid and species	July/August			December/January		
	Av.D. (m)*	Sample size	Nos./ha	Av.D. (m)*	Sample size	Nos./ha
Grid 1						
Arvicanthis niloticus	—	0	0.0	21.16	19	26.8
Rhabdomys pumilio	—	0	0.0	20.60	8	6.1
Total			0.0			32.9
Grid 4						
Arvicanthis niloticus	14.08	19	36.7	10.02	83	116.0
Lemniscomys striatus	?	?	?	12.38	18	28.8
Praomys natalensis	12.35	34	48.0	14.17	26	48.3
Total			84.7			193.1
Grid 5						
Arvicanthis niloticus	13.67	55	77.0	10.88	93	145.6
Praomys natalensis	24.50	5	7.8	11.58	28	32.5
Rhabdomys pumilio	?	?	?	8.50	12	34.1
Total			84.8			212.2

* Av.D. = Average distance between successive recaptures.

is made for underrepresented species, densities range from 100 to over 200 rodents per ha. These densities are probably minimal as there was little evidence of animals ranging far beyond the boundaries of the grids so that the added strip is probably a maximal addition to the area. It is also possible that not all the animals present were trapped.

Grid 1 demonstrates an increase from about one animal per ha in July to a figure approaching 40 in January. On this grid, with twice the interval between traps as on grids 4 and 5, the number of recaptures of *Arvicanthis* is markedly reduced. For example, 35 animals were recaptured 55 times on grid 5 in August, whereas 40 animals were recaptured 19 times on grid 1 in January. This could imply that *Arvicanthis* by having a small home range encountered traps less frequently on grid 1 in which case the figures on Av.D. may emphasize the more extended movements and so provide a relatively high estimate. Should this be so, the density here will be underestimated.

Population Structure

The population structure has been examined for *Arvicanthis* and *Praomys* from body weights and dental attrition. In *Arvicanthis* (Fig. 2) the weight range of 11 to 130 g is represented in both trapping periods. Unlike the dry season data, the July and August figures display a bimodality. The smaller left-hand peak possibly represents animals recruited into the population in the current wet season. Although this bimodality is not evident in the tooth wear data, they do suggest a high recruitment of young animals into the population at this time. Males attain heavier weights than the females. The female appearing in the 111–120 g category in August was pregnant, which added 35 g to her weight. At both collecting periods recruitment had recently been taking place. Furthermore, there were similar proportions of older animals in the two samples.

In *Praomys* (Fig. 3), there is a wider range of weights and tooth wear categories in the wet season sample as this contains a considerable element of animals weighing less than 25 g. The dry season sample has a much more compact structure as indicated by both body weight and tooth wear. By December there is apparently little recruitment and the older group of animals present in August has been lost from the population. This group will presumably be replaced as the main cohort increases in size over the following 6 months.

These differences between *Arvicanthis* and *Praomys* may be partly explained by their different growth and development rates. Taylor and Green (1976) report that in the laboratory *Arvicanthis* attains a weight of 45 g in 3.5 to 4 weeks, whereas *Praomys* takes 6 weeks to attain 25 g. *Arvicanthis* can reproduce at 4 weeks, but *Praomys* takes 3.5 months to reach breeding condition (Johnston and Oliffe, 1954).

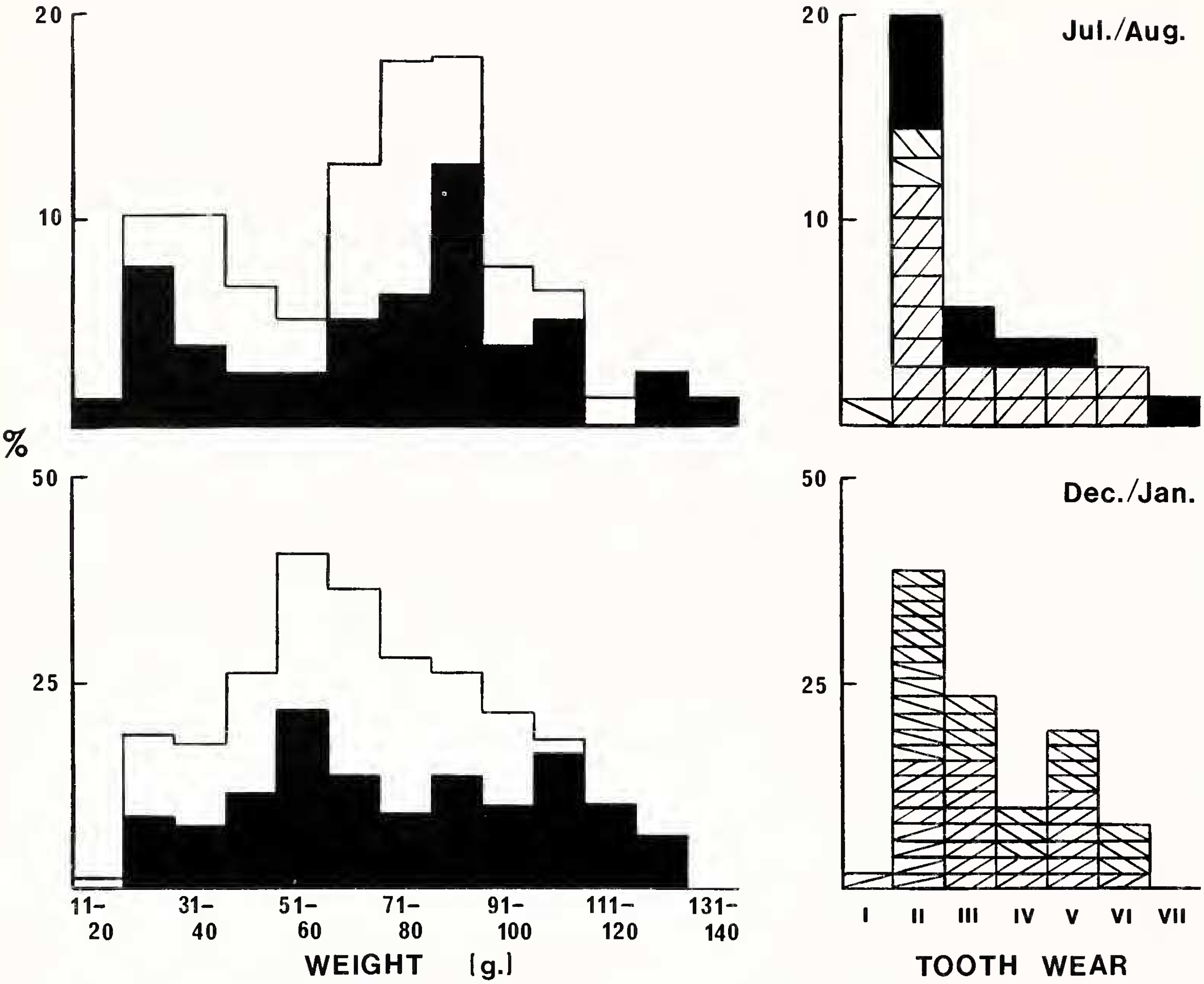

Fig. 2.—Weight and tooth wear distributions and reproductive condition of *Arvicanthis niloticus* in the middle of the wet (July–August) and dry (December–January) seasons. The data on weights include all 276 live and snap-trapped animals. Males and females are represented by solid and open blocks, respectively. The tooth wear histograms are based exclusively on 80 snap-trapped animals. Pregnant females are indicated in solid black, mature females by two lines falling to the right, immature females by one line falling to right, mature males by two lines rising to the right, and immature males by one line rising to the right.

Reproduction

The most comprehensive reproductive data were obtained on *Arvicanthis* and *Praomys* (Figs. 2 and 3). For the remaining species data were scant. Two mature female *Rhabdomys* and *Otomys* were obtained in the wet season; the latter was pregnant with four embryos and lactating. In the dry season two adult female *Rhabdomys* and one *Lemniscomys* were not in breeding condition, whereas the only female *Otomys* and *Lophuromys* collected were both pregnant with three embryos each.

In both *Arvicanthis* and *Praomys* breeding was intense in the middle of the wet season with almost all mature animals reproductively active. The number of embryos in eight pregnant *Arvicanthis* females were five, six, seven, seven, seven, seven, nine, and nine. The only mature female that was not pregnant was lactating and contained 14 placental scars. This animal could have already produced two litters. Although the identification of scars in pregnant animals is difficult, other indicators of the time of the onset of breeding are available. These include the relative age of embryos, lactation, and the recruitment of immatures. Four of the pregnant *Arvicanthis* were in early pregnancy with reproductive tracts weighing less than 2 g. Two of these were

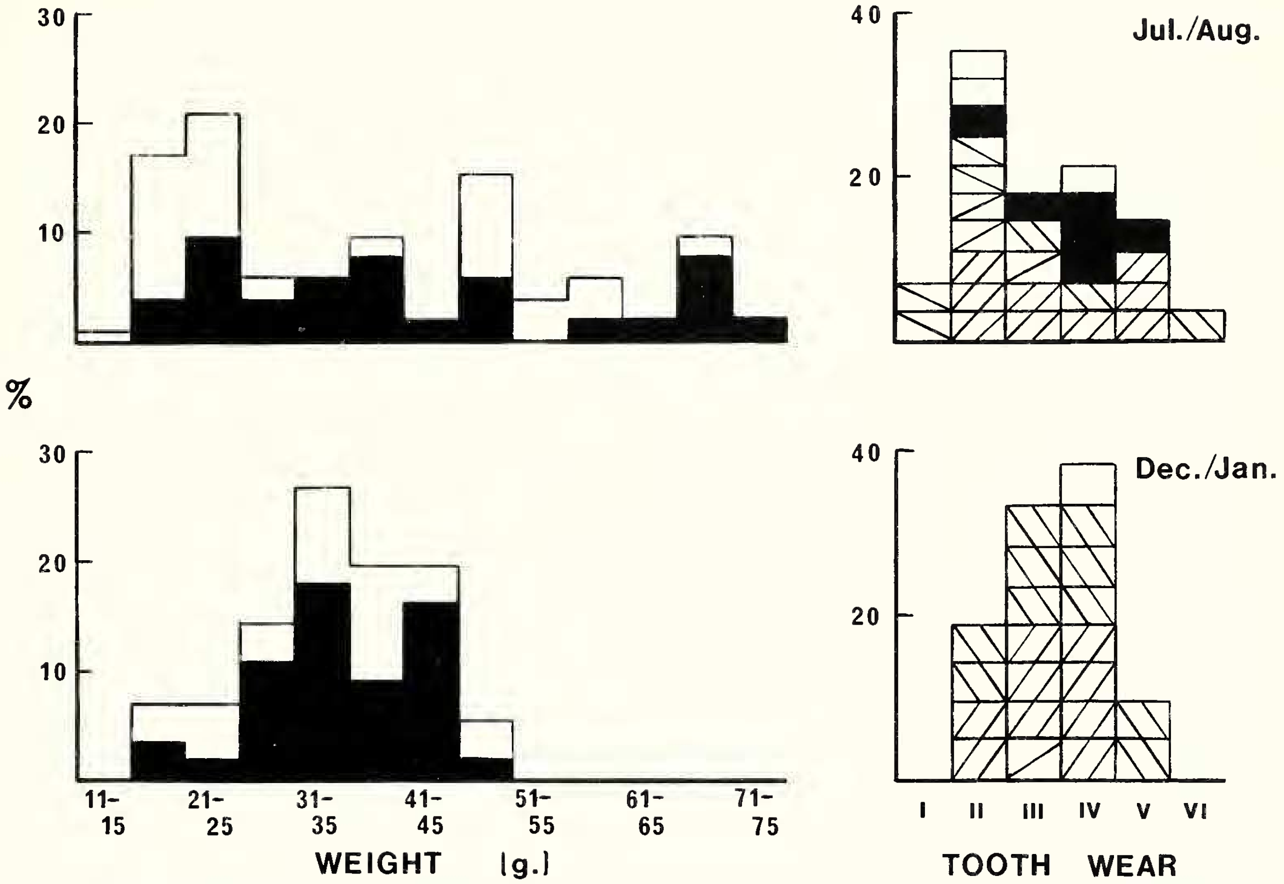

Fig. 3.—Weight and tooth wear distributions and reproductive condition of *Praomys natalensis* in the middle of the wet (July–August) and dry (December–January) seasons. Legend as for Fig. 2. The open blocks in the tooth wear histograms are of unsexed animals. The data on weights and tooth wear are based upon 109 and 49 animals, respectively.

lactating and were probably suckling litters in the nest. In contrast, one female was near full term with her nine embryos each having a mean weight of 3.2 g. On this evidence it appears that breeding must have been under way for approaching two months. The date of termination of breeding is more difficult to ascertain. By early January 11 of 52 animals taken were immature and could have been conceived six to eight weeks earlier. All adult females contained placental scars. These clustered around a mode of four (four, four, four, five, nine, 12, 12, 12, 15, 16) which could suggest an average litter approximating to this figure. This obtains support when only the larger and more prominent scars are included in the counts. The figures for these 10 animals are then five with four scars, three with five, one with six, and one with seven, a mean of 4.8. If these animals were latterly producing litters of this size, they were much smaller than the mean of 7.1 recorded earlier in the year.

Praomys had been reproducing for some time prior to July with 36% of the population comprised of immature, young animals. As with *Arvicanthis*, the impregnated females ranged from the recently conceived to near full term. Embryo numbers for five pregnant females were seven, seven, nine, nine, and nine. By late December, *Praomys* appeared to be well into reproductive anoestrous. Scars were only seen in two of the adult females; they numbered 10 in the one in which they could be counted. Only 5% of this sample were immature, compared to 21% in *Arvicanthis*. These differences are supported by the demographic data. It is of note that reproduction was taking place in young animals with low tooth wear values.

Range Length

As the number of recaptures (Table 4) on the grids were relatively small for the calculation of meaningful home range sizes it was considered that

Table 4.—*Adjusted range lengths.*

Species	Grid	Date	No. of captures 2	3	4	5	6	7	8	9	10	Total	Mean range length (m)	Range (m)
Arvicanthis niloticus	4	Aug	3	1	4	—	—	—	1	—	—	9†	26.50	10–56
Arvicanthis niloticus	4	Dec	12	10	9	2	2	1	—	—	—	36	19.71	5–40.5
Arvicanthis niloticus	5	Aug	—	4	—	3	1	—	1	1	1	11	29.22	12–40.5
Arvicanthis niloticus	5	Dec	11	8	6	7	1	2	—	—	—	35	21.61	10–47.5
Arvicanthis niloticus	1	Jan	12	2	1	—	—	—	—	—	—	15	31.10	10–73.5
Praomys natalensis	4	Aug	3	3	2	—	1	1	1	—	1	12	25.95	5–47
Praomys natalensis	4	Dec	5	4	3	4	1	—	—	—	—	17*	31.41	10–82
Praomys natalensis	5	Aug	1	2	—	—	—	—	—	—	—	3	34.50	21–52
Praomys natalensis	5	Dec	—	—	2	3	—	—	—	—	—	5	27.60	19–50

† Three of these animals were also caught on the adjacent grid 5.

* Seven of these animals were also caught on the adjacent grid 4.

a useful alternative would be the estimation of range length. This involves calculating the distance between the two furthest points of capture and adjusting this figure by the addition of the distance between traps. The mean range length figures for *Arvicanthis* on grids 4 and 5 are smaller in December. The high figure on grid 4 in August was influenced by three animals being occasionally found on grid 5. On grids 4 and 5 in December only three and four animals, respectively, had ranges of more than 30 m. During this period no animal was caught on both grids. These combined data suggest smaller home ranges in December when densities are higher.

The *Praomys* samples for grid 5 are particularly small. The data from grid 4 suggest a small increase in range length in a population showing little change in density from August to December. The increased range length is influenced by the considerable movement between the two grids by this species in December. *Praomys* may be more wide roaming than *Arvicanthis* as during August an animal marked on grid 4 was snap trapped 100 m from it. Cheeseman (1975) found this species had a small compact home range in *Imperata* grassland and a mean adjusted range length of 75 m.

Table 5.—*Catches of rodents in the main vegetation types of grid 5. Figures are expressed as number of catches per trap.*

Species	Date	*Lippia*	Grass and *Lippia*
Arvicanthis niloticus	Aug	1.70	0.65
Arvicanthis niloticus	Dec	1.87	1.47
Praomys natalensis	Aug	0.07	0.18
Praomys natalensis	Dec	0.50	0.43
Rhabdomys pumilio	Dec	0.07	0.33

Distribution on the Grids

With such high densities of rodents populating grids 4 and 5, it is particularly relevant to consider how resources within them might be partitioned. This can be indirectly assessed by the examination of distribution within the grids, assuming that the capture of an animal within a trap is an indication of the animal favoring the environment in the trap's immediate vicinity. This information can be obtained by analyzing the success of each trap and noting its location in relation to the vegetation. On grid 5 the vegetation could be subdivided into two intergrading categories. *Lippia* was present over all the grid, although in some places it was more dominant than others where there was a greater amount of grass. There were then *Lippia* and *Lippia*-grass habitats. It was found that 30 traps were located in the former and 51 in the latter. The total number of catches by traps in these two broad divisions are summarized in Table 5. The results show that in August *Arvicanthis* favored the bushy *Lippia* with more than twice as many catches being made in it than in more grass encroached areas. By December, when the population had almost doubled, the number of catches in the *Lippia* had not increased greatly, whereas elsewhere the increase had been dramatic. As these *Lippia*-grass areas occupied the

Table 6.—*Trap success on grid 4.*

Species	Date	No. of captures in the same trap								Total animals
		0	1	2	3	4	5	6	7	
Arvicanthis niloticus	Aug	65	9	4	1	1	1	—	—	17
Arvicanthis niloticus	Dec	29	16	15	14	4	1	1	1	50
Praomys natalensis	Aug	48	26	2	4	1	—	—	—	20
Praomys natalensis	Dec	49	21	9	2	—	—	—	—	23
Rhabdomys pumilio	Dec	73	4	2	2	—	—	—	—	14
Lemniscomys striatus	Dec	63	12	2	4	—	—	—	—	12

In August 11 traps caught two species: *Arvicanthis/Praomy*, 8; *Praomys/Otomys*, 2; *Praomys/Lemniscomys*, 1.

In December 32 traps caught two or three species: *Arvicanthis/Praomys*, 9; *Arvicanthis/Lemniscomys*, 5; *Arvicanthis/Praomys/Lemniscomys*, 7; *Arvicanthis/Praomys/Otomys*, 1; *Arvicanthis/Praomys/Rhabdomys*, 1; *Praomys/Rhabdomys*, 3; *Praomys/Lemniscomys*, 4; *Rhabdomys/Lemniscomys*, 1.

larger portion of the grid they would be able to spatially accommodate much of the increased population. *Praomys* was caught less frequently in the *Lippia* when in low numbers, but by December when numbers had increased appreciably it was caught almost equally in both vegetation types. *Rhabdomys* was demonstrably more common in the *Lippia*-grass vegetation.

The vegetation on grid 4 formed a complex mosaic, which did not readily permit subdivision into broad categories. The stature of the bush varied within the grid as did its composition. Furthermore, there were grassy patches but these were very small (a few square m) and merged imperceptibly with much of the *Lippia*-dominated vegetation. The grassland along two sides of the grid hardly encroached upon it with the distinction between it and the scrub and bush being quite sharp. In view of this vegetational complexity, the data for this grid was analyzed rather differently to that for grid 5. Table 6 records the catches in each trap. In August, 65 traps made no catch of *Arvicanthis*, nine made one catch, four made two catches, and so forth. For this species only 16 traps were visited and most of these were clustered in one corner of the grid close to a warren. By December, with larger numbers present, 52 traps were visited. The 16 traps catching animals in August made 29 captures; the same traps made 26 captures in December. Thus, as with grid 5, there was a greater utilization of the grid with higher numbers.

Praomys numbers did not change markedly over the 4-month interval between the trappings and at both times this species was widely dispersed, favoring no particular sector of the grid. The 33 traps making all the catches in August obtained 14 of the 45 December catches. The December *Rhabdomys* catches were interesting. They were all made in the two outermost rows of traps along the two sides of the grid bounding the grassland. Most *Lemniscomys* catches were made in the half of the grid remote from the track but the distribution of this species apart from its widespread appearance (three traps in August, 13 in December) is difficult to interpret.

With the increase in numbers of rodents on grid 4 the number of traps catching more than one species almost trebled. By December nearly two fifths of the traps caught animals belonging to two or more species (Table 6). There were eight species combinations caught in single traps with no firm indication of any one species excluding another from a particular location. Whatever the ecological requirements may be of individual species there can be little doubt that on this grid several species must live in close juxtaposition. Furthermore, there is the possibility of appreciable intraspecific interaction when animals occur at these densities. From both grids it is suggested that *Arvicanthis* occupies core areas from which it spreads and that these situations do not increase their densities as breeding takes place.

DISCUSSION

There are several important findings from this exploratory study, which involved three months intensive field work. One of the most striking features is the almost complete absence of small rodents from the swards of open grassland in the middle of the wet season and their relative frequency during the dry season. Not only was this true of the grid trappings. Such removal trappings as were undertaken in grassland in July and August returned negligible catches and it was only if there were herbs, weeds, and some low bush present that trapping improved. This situation raises several relevant issues. The colonization of grassland must have been rapid over extensive areas. If the 1974 and 1975 conditions were typical, and there was no reason for believing they were not, a decline in numbers could be anticipated in the grassland between January and July 1975. That the events of 1974 represented a single and permanent colonization could only be considered possible if there were some special circumstances, such as fire earlier in the year, or a permanent change in ecological conditions, such as an alteration in the grazing regime of cattle. The authors were assured that neither of these occurrences nor any other observable change in ecological conditions had taken place in the previous few years. This being the case, it appears that these small rodents have permanent localized reservoirs of high density populations which, with the onset of breeding, result in a rapid spread and temporary colonization. When first trapped in July 1974, the grasslands appeared most suitable rodent habitats. There was good cover, a diversity of plant species, and a substratum suitable for the construction of burrows. This was well into the wet season and it can only be assumed that at the end of the dry season and early into the rains, the habitat becomes much less hospitable as the grasses die back.

The dry season density of 30 to 40 rodents/ha in the grassland is of the same order of magnitude as the 13 to 64 animals/ha Cheeseman (1975) found in grassland in western Uganda, which he trapped monthly over a period of 19 months. Here populations never approached the low levels obtained at Nakuru. Misonne (1963) estimated there were 65 rodents/ha in *Hyparrhenia* grassland in Zaire, whereas Bellier (1967) found 22 rodents/ha in savanna in the Ivory Coast. The bush-scrub populations of 100 to 200+ animals/ha obtained in this study were higher than all these grassland figures. Work elsewhere in Africa in mixed and arable vegetation indicate that high densities can be obtained. In a crude estimate of numbers in a small, abandoned cultivated plot near Kampala, Delany and Kansimeruhanga (1970) recorded a density of 160 rodents/ha, whereas in eastern Zaire Dieterlen (1967) obtained 454 rodents/ha in an area of grass, bush, and scrub adjacent to cultivated land, which the rodents also exploited. The particular significance of the Nakuru situation is the localization of these populations into extremely small pockets. Within the whole study area, grids 4 and 5 were the only patches of this type of vegetation that were sufficiently large to accommodate the small grids used. Dense vegetation occurred in the lakeside woodland but here the removal trappings caught few animals. Furthermore, this vegetation was not the same as that in grids 4 and 5.

The spread of rodents from their localized dense pockets must be associated with an increase in number through reproduction and the availability of suitable resources. As far as can be ascertained, it appears that reproduction commenced about May and terminated in October or November. It is probable that it was continuous throughout this period although this cannot be stated with certainty. Taylor and Green (1976) have shown that at Kitale *Arvicanthis* begins breeding 2 to 3 months after the start of the rains and ceases approximately a month after their termination. Here, reproduction is greatly influenced by availability of seeds and/or cereals which usually do not become available until 2 or 3 months after the beginning of the rains. The breeding of *Praomys* was also dependent on seeds and/or cereals and had a similar pattern to *Arvicanthis*.

Continuous breeding over several months and the ability of *Arvicanthis* to reproduce at an early age make for considerable increases in population densities. It is suggested that this results in the spread into and exploitation of previously uninhabited areas while the production of the grass seed crop would facilitate breeding within them. Such a spread occurred on a very small scale in grids 4 and 5. On grid 5 the dispersal was from the bush dominated to the more grassy areas, a phenomenon apparently having general application. It is interesting that *Praomys* did not become established in the grassland and furthermore, the numbers caught in the scrub did not greatly differ between the two trapping seasons. It was less numerous on grid 5 where the interphase with grassland was more obvious than in grid 4, which was more bushy. This apparent avoidance of grassland is unusual as this is a habitat in which this species can be numerous (Cheeseman, 1975). The same is true of *Lemniscomys*, which at Nakuru was not very common. More *Rhabdomys* were caught, although, again, this was nothing like as numerous as *Arvicanthis*. It is difficult to identify the vegetation this species occupies in the adverse season as it appears to be absent from grassland and avoiding the scrub. It could resort to the more intermediate situation where grasses and denser herbaceous vegetation meet. The whole study needs extension to consider the ecological requirements of individual species. No examination was made of their food, activity, microhabitat requirement, or social interactions with members of their own and other species. The faunal diversity and population densities make the detailed examination of many of these phenomenon particularly attractive.

There is a further aspect of this study that merits brief consideration. Both *Arvicanthis* and *Praomys* are serious agricultural pests in Kenya (Roberts, 1939; Taylor, 1968) and many other localities in tropical and subtropical Africa (Taylor, 1962, 1969). Their occurrence in large numbers in Kenya can be sporadic (Taylor, 1968), although high densities have been associated with protracted wet seasons and a rich growth of weeds and other vegetation. In contrast, Taylor and Green (1976) reported *Arvicanthis* absent from their study area in agricultural land at Nakuru for a year. Thus, while this species can be very abundant, it is also sensitive to habitat conditions, which account for its temporary disappearance from large areas. At such times it is probably confined to small nuclei with good cover and adequate food supply. The agricultural environment, particularly where there is cultivation, is unstable and is unlikely to afford good permanent habitation for rodents. However, the retention of small habitable nuclei provide potential reservoirs for establishment over larger areas. The removal of small, unused pockets of scrub and bush would do much to prevent infiltration into cultivated crops. The same could well apply to badly maintained smallholdings where weed growth is permitted and cover for rodents is thereby inadvertently provided.

SUMMARY

The field work was carried out in Nakuru National Park, Kenya, during the middle of the wet (July and August 1974) and dry (December 1974 and January 1975) seasons. The rains occurred from March to November. Trappings were concentrated in mixed, ungrazed grasslands (*Hyparrhenia, Themeda, Chloris*), and small adjacent areas of scrub in which *Lippia javanica* was an important species.

Most of the live trapping, using 81 large Sherman traps, was in three grids (9 by 9 traps), one in grassland and two in scrub. The latter were 21 m apart and had trap spacings of 5 m; the former had a trap spacing of 10 m. Each grid was trapped in both wet and dry seasons. Snap trapping was undertaken in other parts of the study area.

Arvicanthis niloticus and *Praomys natalensis* were caught most frequently; *Lemniscomys striatus, Rhabdomys pumilio,* and *Otomys angoniensis* were obtained in small numbers and *Dendromus, Mus minutoides, Aethomys,* and *Lophuromys* recorded occasionally. The grassland supported negligible populations in July. During August densities in the scrub approached 100 rodents/ha. By December populations in the latter had increased to 200/ha and in the former 33/ha.

Both wet and dry season populations of *Arvicanthis* contained animals of a wide range of ages. In contrast, the *Praomys* population contained few older animals in December. Reproductive activity was intense in the wet season and virtually nonexistent in the dry season.

At the higher dry season density there was an indication of smaller home ranges in *Arvicanthis.* This species then occupied more extensive areas of the grid than previously. Such dispersal could be a factor accounting for the prevalence of this species in the grassland at this time.

Praomys was frequent in scrub where it was much less numerous than *Arvicanthis;* it was uncommon in grassland. *Rhabdomys* was typically found in this vegetation. The small patches of scrub within the grassland apparently supported reservoir populations of *Arvicanthis,* which, during the reproductive phase, expanded into adjacent grassland.

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MODERN RODENT FAUNA OF THE LOWER OMO VALLEY, ETHIOPIA

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ABSTRACT

One hundred and seventy rodents, comprising 15 species of nine genera and five families (Sciuridae, Gerbillidae, Cricetomyidae, Muridae, and Gliridae), have been captured in the lower Omo Valley. These represent a good sampling of the modern rodent population of the several biotopes of the areas—Sahelian savanna, arid zones (paleontological beds), and forested blocks comprising a continuous stratum of large trees and associated bushes and shrubs.

INTRODUCTION

One hundred and seventy rodents, comprising 15 species of nine genera and five families, were captured in the lower Omo Valley in the summer of 1973 during the paleontological expedition organized by Yves Coppens. These represent a good sampling of the modern rodent population of the several biotopes of the areas.

The specific designation of certain species mentioned here cannot always be regarded as definitive, because systematic revisions may be required. However, their ecological characteristics are well-defined. A future study, based on karyotypes, will permit the systematics of species to be more firmly established.

Animals have been captured in various ways—through excavation of their burrows; by hand at night with the aid of a light; by traps set at burrows or in lines and baited with peanut butter; or by large metal cans sunk half to three-quarters of a m into the ground.

RESULTS

Species List

Sciuridae
- *Heliosciurus gambianus omensis* (Thomas, 1909)*
- *Xerus rutilus* (Cretzschmar, 1826)

Gerbillidae
- *Tatera nigricauda* (Peters, 1878)
- *Tatera minuscula* Osgood, 1936
- *Taterillus harringtoni* (Thomas, 1906)
- *Gerbillus pulvinatus* Rhoads, 1896
- *Gerbillus pusillus* Peters, 1878

Cricetomyidae
- *Saccostomus mearnsi* Heller, 1910

Muridae
- *Mastomys erythroleucus* (Temminck, 1853)
- *Arvicanthis niloticus* (Desmarest, 1822)
- *Arvicanthis somalicus* Thomas, 1902
- *Acomys percevali* Dollman, 1911
- *Acomys wilsoni* Thomas, 1892
- *Thamnomys dolichurus* (Thomas and Wroughton, 1908)**

Gliridae
- *Graphiurus murinus* Desmarest, 1822

*Captured by A. Duff-Mackay (National Museum, Nairobi, in 1967).

**Captured by F. Rhodain and R. Houin.

The presence of at least two other species is indirectly documented. An immense network of burrows, 3 to 5 cm in diameter, situated at a depth of about a meter, occurs on the surface of the Kibish Formation sediments, and may well testify to the presence of a bathyergid mole-rat. Some nests, filled with dry leaves, and unlike those of *Graphiurus* or of *Thamnomys,* were found situated either in hollow limbs or in the empty trunks of certain trees in the gallery forest and could well belong to a species of *Thallomys,* a genus already documented elsewhere in Ethiopia (Petter, 1973).

DISCUSSION

Geographic Distribution

Some species are widely distributed throughout sub-Saharan Africa (*Arvicanthis niloticus, Mastomys erythroleucus, Thamnomys dolichurus, Graphiurus murinus*). Others are restricted to eastern Africa (*Xerus rutilus, Tatera nigricauda, Taterillus*

Table 1.—*Number of rodents collected in the five ecological zones of the trapped area in the Omo Valley, Ethiopia. The number of trap-nights is indicated for each zone, but is not significant because some species were collected by digging their burrows or by sunken can-traps.*

	Riverine areas		Arid zones		
Species captured	With trees & shrubs	Without trees, with grass & thickets	Slopes	Bottom	Plateau
Xerus rutilus				1	5
Tatera nigricauda	4	11		2	8
Tatera minuscula				2	1
Taterillus harringtoni		1		2	3
Gerbillus pulvinatus					27
Gerbillus pusillus				3	6
Saccostomus mearnsi		9			
Mastomys erythroleucus	2	3			
Arvicanthis niloticus	11	2			
Arvicanthis somalicus		7		5	
Acomys percevali		4	3	16	3
Acomys wilsoni	2	16			9
Total specimens	19	53	3	31	62
Number of trap-nights	640	1,880	290	630	1,711

harringtoni, Saccostomus mearnsi, Arvicanthis somalicus, Acomys wilsoni). Others appear to be more or less endemic and limited in distribution to southern Ethiopia and northern Kenya (*Heliosciurus gambianus omensis, Tatera minuscula, Gerbillus pulvinatus, Gerbillus pusillus, Acomys percevali*).

Ecological Aspects

These taxa differ in their biology. Certain species dig burrows and are active nocturnally (*Mastomys erythroleucus*) or diurnally (*Xerus rutilus*). Others are active both day and night and construct nests of dry vegetation at the foot of bushes or in high grasses (*Arvicanthis* spp.). Still others are arboreal and active during the day (*Heliosciurus gambianus omensis*) or the night, and construct nests of dry leaves in hollow limbs (*Graphiurus murinus*) or attach them to bushes or lianas (*Thamnomys dolichurus*). Their nests do not seem to be occupied throughout the year.

Three major habitats may be usefully distinguished (see Table 1). The riverine area has two aspects—with trees and shrubs (including *Trichilia roka, Tapura fischeri, Ficus sycomorus, Celtis integrifolia, Ziziphus rubescens, Cordia gharuf*) forming a continuous canopy, and with lianas (*Sissus, Sabia*) present. This zone appears to have a poor rodent fauna; only *Heliosciurus gambianus omensis, Graphiurus murinus,* and *Thamnomys dolichurus* have been captured. Native villages situated here harbor *Arvicanthis niloticus* and *Mastomys erythroleucus.* There is also the riverine zone, largely without trees, but with grasses and very dense thicket. Here *Mastomys erythroleucus, Saccostomus mearnsi, Acomys wilsoni,* and *Tatera nigricauda* occur. The soils of this zone are heavy and clay-like and often appear as vertisols. The later zone is flooded at more or less regular intervals in keeping with the Omo flood regime.

The Shungura Formation exposures may be considered separately and to have three aspects. The slopes of the exposures are comprised of detritus and eroded Plio-Pleistocene sediments. This very arid facies, practically without vegetation, harbors *Acomys percevali.* The cuestas of these exposures, which are covered with tuffs, and the bottoms, which separate them and contain recently eroded sediments, still have a very arid vegetation comprised of open shrubs (*Euphorbias, Adenium obesum, Cissus rotundifolia, Dasysphiera prostrata, Commiphora africana, Adenia venenata, Caralluma russelliana, Sesamothamnus brisseanus,* and *Maerua crassifolia*) and rare herbaceous plants (*Indigofera* sp., some Cyperaceae). In these situations *Gerbillus pusillus, Taterillus harringtoni, Tatera minuscula, Arvicanthis somalicus,* and *Xerus rutilus* occur.

Finally, the plateau has several soil types, more or less rich in clay, and these have a considerable influence on the local composition of the vegetation, generally that of a more or less open shrub or bush savanna (*Acacia paolii, A. reficiens, A. horrida, Grewia tenas, Cadaba glandulosa, C. gilletti, Sciatula hortacantha, Serricomopsis pallida*) with herbs (*Blepharis persica, Polygala erioptera, Ipomea belpharosepala*) as well as numerous grasses (*Aristida, Cenchrus, Chloris, Dactyloctenium*, and others). The plateau rodents are *Xerus rutilus, Acomys wilsoni*, and *Arvicanthis somalicus*, which occur everywhere, and *Gerbillus pusillus* and *G. pulvinatus* which occupy areas of lighter, more sandy soil than those where *Taterillus harringtoni* and *Tatera nigricauda* are found.

The distribution of these various rodent species, which utilize the part of the environment which best agrees with their ecological preferences, is further affected by another limiting factor—dryness—which is more or less strongly pronounced according to the year and the season. Except for the gallery forest species, the rodent fauna is rather characteristic of dry, and even arid zones. The low incidence of species in the gallery forest is a result of recurrent dry periods that prevent the occurrence of species that are linked to a permanently moist environment and in addition the occasional flooding of the entire area, thereby restricting immigration by burrowing or purely terrestrial species.

Reproduction

Observations made during the summer of 1973 broadly confirm the conclusions of previous workers (Dieterlen, 1967; Happold, 1966; Poulet, 1972; Hubert, 1977) on the reproduction of tropical rodents in sub-Saharan Africa. Reproduction occurs some weeks after onset of the rainy season. The onset of rains in early July 1973, in the north Shungura area, saw active reproduction of the principal rodent species represented there. In August, 80% of the trapped females were sexually active—either in estrous, gestating, or lactating. Farther south, on the other hand, in the Kalam area, where rain was lacking, there was no evidence of reproductive activity among those rodent populations.

Taxonomic Comments

The modern rodent fauna of the Lower Omo Valley is typical for this area in Africa, where different types of habitat are represented—Sahelian savanna, arid zones, and forested blocks comprising a continuous stratum of large trees and associated bush and shrubs.

There are two squirrels, one arboreal (*H. g. omensis*, described from this place) and one fossorial (*X. rutilus*). Two species of *Tatera* are present, one widely distributed in eastern Africa (*T. nigricauda*), and a very small one, endemic to this area, *T. minuscula* (which was described by Osgood in 1936 from specimens collected in a nearby area, the Webbi Shebelli in southeastern Ethiopia, and was never officially collected since that time). *Taterillus harringtoni* occurs in all this part of eastern Africa (Robbins, 1975) where it lives together in the Sahelian savanna with two species of gerbils, a medium-sized hairy-footed species, *G. pulvinatus* (Hubert, 1978; Schlitter, personal communication) and a small one with naked sole, subgenus *Hendecapleura, Gerbillus pusillus* (Roche, 1976). *Saccostomus mearnsi* is the northern form of this genus, occuring in Ethiopia, Uganda, Kenya, and Tanzania (Hubert, 1978). The *Mastomys* seems to be referable to *Mastomys erythroleucus*, a large species characterized by a light gray belly, a brown-yellowish back, and a karyotype of 38 chromosomes, occurring in western and central Africa (Petter, 1957 and 1978). Two species of *Arvicanthis* are represented—*A. niloticus*, a large species, which is found in wet areas in the savannas over all Africa, and *A. somalicus*, a smaller one with a paler fur, from the arid zones of eastern Africa. The two species of *Acomys* were reported from this area by Matthey (1968).

CONCLUSIONS

It is worth noting that four of the nine rodent genera present in the lower Omo basin are represented each by two species adapted to slightly different habitats. Here is an adaptative evolutionary process of some plasticity frequently found in various animal species. It permits maximum utilization of the heterogeneity of the environment, in space and in time. This strategy, reflected in more or less marked specialization of different species, adapted to particular conditions, contrasts with that of species substantially less strict in their ecological requirements. However, those latter species are capable of very rapid occupation of various habitats given some favorable change of a seasonal or other unusual nature.

Thus, the modern rodent fauna of the Lower Omo basin is rich, reflecting the different habitats present, which is characteristic of the African tropical zones, even the dry zones.

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EVOLUTION OF THE RODENT POPULATION OF A DRY BUSH SAVANNA IN THE SENEGALESE SAHEL FROM 1969 TO 1977

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ABSTRACT

An eight-year study of changes in rodent populations in a Sahel savanna habitat in northern Senegal is presented. Characteristics of population dynamics for the principal species that are most important in allowing repopulation of dry bush savanna areas include the ability to rapidly attain high population levels after an initial reinvasion. Habitat preference and resource utilization within the dry bush savanna are critical factors to successful increase in population levels and their maintenance.

INTRODUCTION

The evolution of small rodent populations was followed in a Sahel savanna in northern Senegal from 1969 to 1977. Trappings were effected at more or less regular intervals (every one to three months) for the following purposes: to determine the composition of the population and its eventual temporal variations; and to determine the most important characteristics of population dynamics for the principal species, including periodicity and magnitude of reproduction, and maximal and minimal densities during the yearly cycle.

The first part of this study, included in the International Biological Program from 1969 to 1972, occurred during an extreme drought which peaked in 1972. Rainfall since that time, although still below 30-year averages, has increased throughout the Sahel. Biological phenomena have thus undergone a renewal, illustrated by the more or less generalized outbreaks of insects and especially rodents in 1975–1976.

The purpose of the present report is to describe this latter phenomenon in a natural environment and to establish a qualitative and quantitative comparison with observations made during the period of drought. These observations were localized to the Sahel savanna of Fete-Ole, in northern Senegal (northern Ferlo).

Average yearly rainfall of about 300 mm supports a dry bush savanna, established on old dune reliefs whose topography governs the distribution of vegetation, which includes large grassy areas with occasional trees on the dunes and dense bushy undergrowth in interdune depressions.

The rainy season lasts only three or four months, between July and October. The rest of the year is dry, becoming chilly from November to March and hot from April to June. Rainfall from 1969 to 1976 is shown in Table 1. Biological activity is concentrated in the rainy season and the first part of the dry season. The majority of the animals reproduce during this period. Animals with an annual cycle, such as rodents, generally reach their abundance maximum between October and January. Population densities then decrease, reaching their minimum just before or at the onset of the rains of the following season. The characteristics of a given annual cycle are thus functions of both the minimum density of the preceding year and the peculiarities of the present reproduction (length and fecundity), all of which determine the growth level of the population and thus the maximum annual number of individuals in the population.

The rodent population of Fete-Ole was studied from 1969 to 1972 and the population dynamics of the most abundant species, *Taterillus pygargus*, was established (Poulet, 1972*a*, 1972*b*). Other studies concerning the effects of the drought were performed in 1972 and 1973 (Poulet, 1974). The spectacular change in the rodent population was studied

Table 1.—*Annual Rainfall in Fete-Ole from 1969 to 1976 (in mm).*

Year	Amount of rainfall
1969	321
1970	209
1971	202
1972	33
1973	209
1974	316
1975	311
1976	343

extensively from 1975 to 1977 by samplings performed during the dry season in order to obtain information concerning the fauna and demography of the region. The detailed analyses of these data are forthcoming (Poulet and Poupon, 1978; Poulet, in preparation).

DISCUSSION

Rodents of Fete-Ole

Gerbillidae.—The most common rodents on the Fete-Ole Sahel are *Taterillus*. *T. pygargus* is found in all the habitats, but this species is the only one which is capable of permanently occupying the dunes, because it is particularly adapted to the sandy habitat. *T. gracilis*, which is much more rare, inhabits only the bushy depressions. The two species coexist in these depressions, but *T. pygargus* consistently is the dominant species. This situation explains why *T. gracilis* appears to have virtually disappeared during the drought, a condition that is much more unfavorable to it than to *T. pygargus*.

Desmodilliscus braueri is a small subdesert rodent, which is very difficult to study because it does not enter the traps. Its presence is known by its occurrence in pellets of owls and, although difficult to trap, it may be stalked at night and caught by hand. Its abundance apparently varies inversely with that of all the other rodents; it is rare during periods of abundant rainfall and becomes more numerous during droughts. It seems to have dissappeared since the outbreak of the other rodents in 1975–1976.

A *Tatera* with 52 chromosomes appeared in 1976 at the latitude of Fete-Ole but its occurrence must be considered as exceptional. Its appearance seems to be exclusively related to a temporary extension of the area of distribution of the species toward the north following the outbreak of 1975–1976.

Muridae.—*Arvicanthis* and *Mastomys* are usually not found in the Fete-Ole Sahel; *Arvicanthis niloticus* normally inhabits the campsites of nomads and *Mastomys erythroleucus* is occasionally found in certain permanent settlements of the Sahel. *Arvicanthis* invaded the Fete-Ole savanna in the rainy season of 1975. Family groups inhabited all the depressions with bushy covering and often adopted a diurnal arboreal behavior. *Mastomys erythroleucus* also inhabited the depressions but was less abundant than *Arvicanthis*. The samples taken revealed only several individuals per depression.

Pullulation of Taterillus

Following the rains of 1974, thus two years after the great drought, the rodent density had risen to a level comparable to that of 1969–1971. There are no precise data for this period but the several *Taterillus* captures made indicated a considerable reproduction beginning in the months of October. The possibility of a rapid growth of rodent populations was indicated by the abundance of herbaceous vegetation as well as acridian multiplication. Population samplings were undertaken in January-February, April, and July of 1975 and then in February, April, and June 1976 (Table 2).

A maximum of population density was reached in April 1975, with approximately 40 *Taterillus* per ha. The reproduction season, at least 6 months long, resulted in the appearance of two successive generations, thus considerably increasing the population density. The period of population decrease resulting from the arrest of reproduction at the end of the dry season was very brief; from July 1975 onward, reproduction recommenced at already high densities, approximately 30 individuals per ha with an average of eight young per litter.

Considering an overall mortality rate of 15 to 20% per month and two successive litters of eight and six young with a starting density of 30 per ha, we may calculate an average maximum density of 180 (135–250) at the end of September. The demographic analysis of samplings of February 1976, show that reproduction during the rainy season of 1976 was indeed very short and that no new individuals appeared beginning with early October 1975. The period of population decrease in 1975–1976 was thus very long (October 1975–August 1976) and the population density decreased from 70 per ha in February to 30 in July, representing an overall mortality rate of 25% per month.

The 1976–1977 reproduction season began rather late, toward the end of September. The annual minimum density was reached at this time, with 20 individuals per ha, a level which is still considerable. The pullulation period could be considered as virtually terminated, because the following cycle showed neither as great a difference between minimum and maximum densities nor as rapid a variation of numbers of individuals.

The pullulation thus occurred in two stages—1) a progressive but important rise in the population

Table 2.—*Estimation of densities and biomass of* Taterillus pygargus *on the dunes of Fete-Ole during the rodent outbreak of 1975–1976. Average weight of an individual is 36 g.*

Date	Density (individuals/ha)	Biomass (g/ha)
January–February 1975	29	1,044
April 1975	40	1,440
July 1975	28	1,008
February 1976	86	3,096
April 1976	54	1,944
June 1976	28	1,008

level, due to a very long reproductive season, followed by a period of population decrease which was too short to bring the density to a low level (1974–1975); and 2) a following reproductive season characterized by a highly elevated fertility which affected the already elevated population level. The outbreak ensued and the population was quadrupled from the first litter (1975–1976).

The abrupt population increase during the second phase led to an overpopulation whose first and foremost effect was to rapidly block reproduction. Because the vegetation did not yet have the time to be degraded, the block had to be at the behavioral level; the promiscuity of individuals was reduced, thus inhibiting all subsequent gestations.

In spite of the abundance of *Taterillus*, mortality during the entire period of population decrease remained limited to a low level of 20% per month. There were no changes in the size of each age group noted between the beginning and the end of the dry season; there was thus no state of famine.

The *Taterillus pygargus*-Sahel savanna relationships appear to be especially well in equilibrium. Just as the great drought of 1972 had no irreversible consequences for the *Taterillus* population, the rapid reproduction of 1975–1976 did not lead to any considerable degradation of the habitats. It may be considered that *Taterillus pygargus* is very suitably adapted to the dry bush environment of the Senegalese Sahel. This does not, however, mean that the outbreak of *Taterillus* was without repercussions. Seed productivity in the savanna and the details of the granivorous diet of rodents are poorly known. It is not possible to precisely estimate vegetation changes, which, although not spectacular, could nevertheless be important. Furthermore, the competitive relationships among consumers were probably changed. Thus, the exceptional abundance of rodents could furnish an explanation for the disappearance of all reproduction among certain granivorous birds, which previously reproduced quite satisfactorily at the end of the dry season (the case of certain species of turtle-doves; G. Morel, personal communication).

Invasion by Arvicanthis niloticus

The invasion of the Sahel savanna by *A. niloticus* at the end of the 1975 dry season resulted from massive migrations induced by an overpopulation at the moment of the maximum population density at the first phase of the pullulation in cultivated areas and in the villages where *Arvicanthis* lives permanently.

The intense reproduction of the newcomers, inhabiting the bushy depressions, explains the spectacular increase in the number of *Arvicanthis* between October and December 1975. The dietary requirements of a population exceeding 100 individuals per ha of habitat and a resulting biomass greater than 11 kg, are such that a state of famine could not be long in developing. The consequences of this chain of events were a significant reduction in physical parameters of the individuals of a given age (size and especially weight), a lifespan not exceeding 9 months due to an intense mortality and a very clear degradation of the woody stratum. Mortality was amplified by predation resulting from abnormal concentrations of diurnal Palearctic birds of prey.

Table 3 shows the population densities in the Sah-

Table 3.—*Estimation of densities and biomass of rodent populations of "bushy depressions" in 1976.* Taterillus *sp. represents* T. pygargus *and* T. gracilis *in a 60:40 ratio. Values are given in ha of effective biotope, that is, ha of bushy depression.*

	Taterillus sp.			*Arvicanthis niloticus*		
Date	Density/ha	Average wt (g)	Biomass/ha (g)	Density/ha	Average wt (g)	Biomass/ha (g)
February 1976	66	38	2,508	100	112	11,200
April 1976	32	38	1,216	73	98	7,154
June 1976	15	38	570	17	84	1,428

Table 4.—*Maxima and minima of population densities, in number of* Taterillus pygargus *per ha of Sahel savanna, for each annual cycle from 1969 to 1977. The average value of population density is calculated from the maximum assuming a constant decrease of 20% per month until the minimum. The average weight of a* T. pygargus *is estimated as 36 g and its daily seed comsumption at 3 g. x = very low density.*

	Annual maximum		Annual minimum				
Date	Date	Density	Date	Density	Average density	Biomass (g)	Seed
1969–1970	April 1970	9	August 1970	4.1	6	216	6,480
1970–1971	October 1970	7.8	August 1971	0.6	3.2	115	3,456
1971–1972	November 1971	0.7	?	x	0.3	11	324
1972–1973	—	—	—	—	x	—	—
1973–1974	—	—	—	—	?	—	—
1974–1975	April 1975	40	July 1976	30	29.5	1,062	31,860
1975–1976	September 1975	180	September 1976	20	83	2,992	80,773
1976–1977	December 1976	45	July 1977	10	23.4	842	25,272

el depressions during the dry season of February to June 1976 for *T. pygargus* and *T. gracilis* (in a 60:40 ratio) and for *Arvicanthis niloticus*. The invasion was massive but was reduced very rapidly. In reality it affected only the "pond" biotope (bushy undergrowth in depressions), which represents only 10% of the Fete-Ole surface. It may be concluded that the permanence of the *A. niloticus* population in the dry bush savanna is questionable, which is fortunate for the natural environment as it can tolerate the presence of these murids for only a short time without irreversible damage.

CONCLUSIONS

The frequent droughts in the Sahel do not enable permanent populations of murids to be maintained in the dry bush savanna. The particular circumstances of an exceptional demographic outbreak are required for the murids to invade this zone. These new populations are nonetheless not capable of maintaining themselves, because of the unacceptable disequilibrium they impart to the habitats they invade. The invasion of *Arvicanthis niloticus* and *Mastomys erythroleucus* in the dry bush Sahel savanna represents the limits of their ecological potentialities; they must be considered not as normal dwellers but rather as invarders with deleterious actions.

Taterillus, especially *T. pygargus*, are the characteristic animals of the Sahel savanna. They may undergo enormous variations in abundance without producing irreversible disequilibrium in the habitats. Table 4 summarizes data gathered between 1969 and 1977 concerning minimum and maximum population densities, biomass, and seed consumption.

Biomass was increased by a factor of 300 between the drought of 1972 and the maximum population outbreak of 1976. These are extreme cases, related to climatic extremes of the Sahel. True Sahel species are those capable of undergoing large variations in population numbers in the absence of irreversible repercussions, neither to the species itself nor to the sheltering environment. This is indeed the case for *Taterillus* but not for *Arvicanthis*.

Seed productivity of 1 ha of Fete-Ole Sahel has been estimated at 29 kg (Bille, 1977). Availabilities from previous years bring the reserve to 40 to 60 kg. These figures are largely in excess of the needs of *Taterillus* during a drought, but it must be supposed that availabilities of the environment in 1976 were at least double, because the quantity of seeds required to support a *Taterillus* population estimated at 80 per ha is about 80 kg. This represents an indirect confirmation of the opinion of Bille, according to which, after the dry period, there is "a compensatory phenomenon enabling the very rapid biological rise of the ecosystem, both for the trees and grasses."

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HABITAT HETEROGENEITY AND CHANGES IN SMALL MAMMAL COMMUNITY STRUCTURE AND RESOURCE UTILIZATION IN THE SOUTHERN KALAHARI

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ABSTRACT

The small mammal communities occurring in four habitats in the southern Kalahari from 1970 to 1976 were examined. Changes occurred in species diversity, and marked fluctuations in the population densities of different species were evident. This led to changes in habitat-niche dimensions, and the amount of habitat-niche overlap between species. Most species also showed changes in food-niche dimensions between winter and summer.

INTRODUCTION

Previous studies on small mammals in the southern Kalahari (Nel and Rautenbach, 1975) have shown that habitat selection occurs in some species, and that it is presumably related to factors such as soil texture and the amount of cover present. Trapping results also revealed that the structure and composition of small mammal communities were different in different habitats at any given time, and that within-habitat changes were common from year to year.

Additional data have allowed a more detailed analysis of changes in the small mammal community occurring in the dry bed of the Nossob River, as well as an attempt to quantify some dimensions of the niche each species occupies. The assessment of niche dimensions is made difficult because of the constant changes in species present, and therefore (presumably) changes in manner and context of interactions between species. This inevitably would lead to changes in niche dimensions and even possibly the amount of competition for available resources. However, even though the available data do not permit an absolute picture of niche occupation to be constructed, some idea may be gained of resource partitioning by small mammals in a subdesert environment.

STUDY AREA

A detailed description of the study area in the Nossob River valley, Kalahari Gemsbok National Park, has appeared elsewhere (Nel and Rautenbach, 1975). Briefly, it covers the low dune forming the west bank of the river, the actual riverbed (usually dry), a raised plateau, and the high dune forming the eastern bank. The low dune consists of white-red consolidated sand, with a cover of "driedoring" bushes, *Rhigozum trichotomum* Burch., some perennial grasses, and a few camelthorn trees, *Acacia erioloba* E. Mey. The riverbed, of fine consolidated silt, is flanked by tall *A. erioloba* trees, has some bushes, such as *Galenia africana* L., occurring, and usually a good grass cover. The plateau, of white calcareous sand, has a sparse ground cover, which gradually increases where it merges into the high dune, which has a vegetation rather similar to that of the low dune.

As rainfall figures are only available from 1966 onward, average annual rainfall (272 mm) is perhaps misleading at this stage; Fig. 1 shows that over the study period the annual rainfall varied a great deal, from 110 mm in 1970 to >550 mm in 1976. Rainfall normally occurs as sharp, localized showers. As is common in desert or subdesert regions, daily and annual temperature fluctuations are severe; temperatures can drop to −10°C in winter (though seldom for more than a few nights per season) and reach 47°C in the shade in summer.

MATERIAL AND METHODS

A trapline of 37 stations, 20 m apart, and extending from the low dune, through the riverbed and plateau, and up the high eastern dune, was laid out in December 1970. Trapping sessions were generally six months apart, and during each session three traps (a Museum Special snap trap, a Victor or McGill rat snap trap, and an aluminum Sherman live trap) were put down in a 1 m radius of the trap station, and kept baited and set for 3 days and 4 nights. Taking each 12 h period as a "trapnight," this gave a total of 21 trapnights (7 "nights" × 3 traps) per station, or 777 trapnights per trap session for the whole trapline. All animals caught were removed and live captures released 3 km beyond the study area. As the width of the arbitrarily separated habitats (low dune, riverbed, plateau, high dune) differed along the transect, 10 trap stations were within the boundaries of the low dune habitat, giving 210 trapnights/session; nine in the riverbed, giving 189 trapnights/session; 11 in the plateau, giving 231 trapnights/

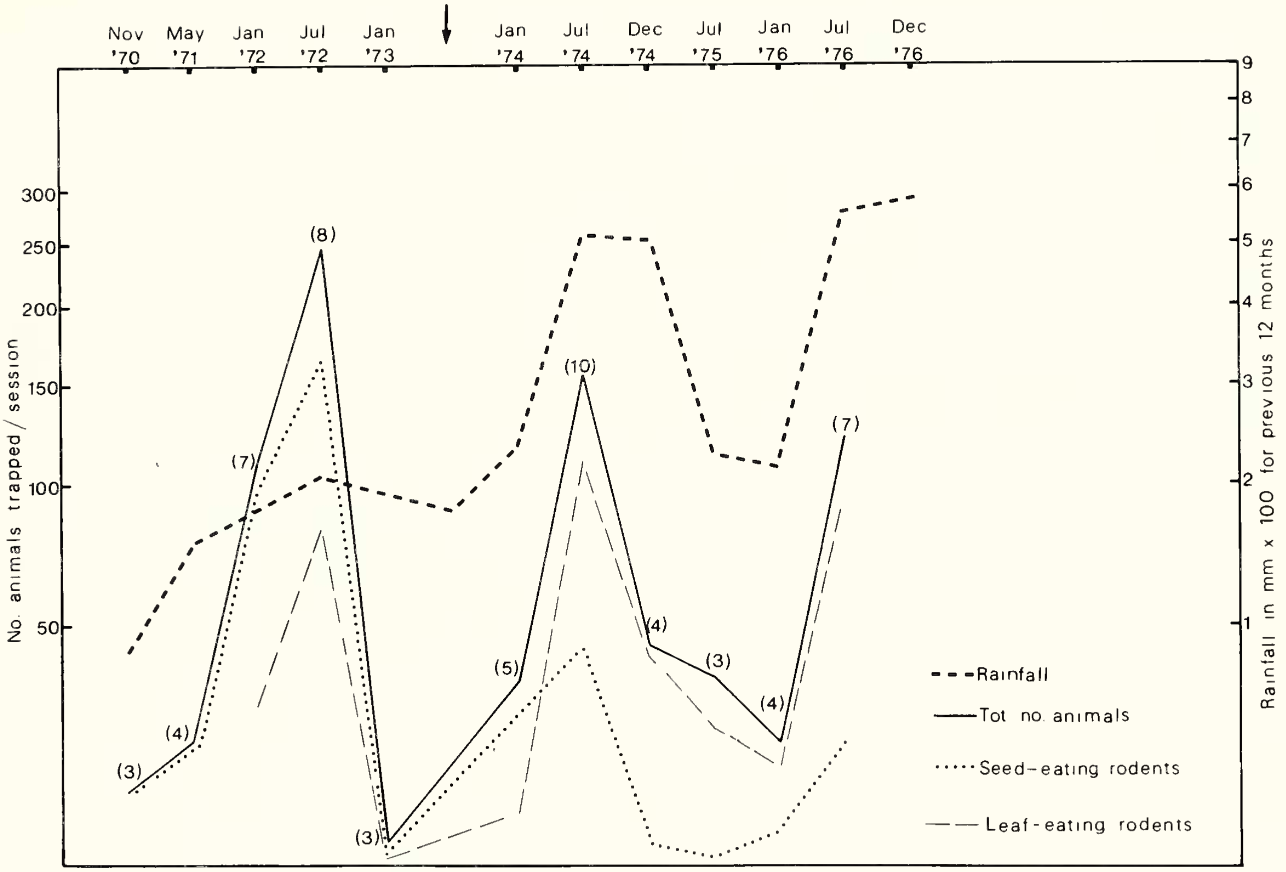

Fig. 1.—Total number, and number of seed-eating and leaf-eating rodents trapped at different periods in the Kalahari Gemsbok National Park. Number of species in parenthesis.

session; seven in the high dune, giving 147 trapnights/session. For comparative purposes, captures were recalculated as per 100 trapnights, either for particular trap stations (see calculation of habitat-niche breadth below) or for a particular habitat.

Without discussing in detail the best concept of a niche it should be noted that here it is regarded in the Hutchinsonian sense, that is being a n-dimensional hypervolume with quantification possible by measuring resource utilization along several axes. In the discussion below the niche referred to is the realized niche.

Data on distribution of the various species in the four habitats accrued from an analysis of captures at the trap stations, regarded here as each representing a different microhabitat.

Data on food preferences were obtained by analyzing stomach contents. Volumetric content and wet weights were noted, and several samples from each stomach were drawn off, shaken with water, and placed in a petri dish for subsequent determination of percentage occurrence, using a Wild M5 stereomicroscope with graticule eyepiece. In the absence of a reference collection of plant cuticles, vegetable matter was classified only as "white" (seeds, roots, and stems) or "green" (leaves). Insect material was not identified to taxonomic groups.

Activity measurements were obtained in the laboratory for only three species, during late March–April. A four-chamber, activity-measuring cage was used (for details see Davis, 1972). Individual activity bouts were recorded on a moving strip chart in an Angus-Esterline event recorder, and subsequently analyzed as to the number of bouts per hour.

The above data were used to calculate diversity indices (and evenness of spread) for each habitat, and for the whole transect, using the Shannon-Wiener formula

$H' = -\Sigma\, p_i \log_2 p_i$ in the form (after Lloyd and Ghelardi, 1963)

$$H' = C\left[\log_{10}N - \left(\frac{1}{N}\sum_{i=1}^{s} n_i \log_{10} n_i\right)\right]$$

where $C = 3.3219$ (a constant) to convert $\log_2$ to $\log_{10}$. This measure for diversity was selected in preference to others (for example, the Brouillin formula) as the data collected represent only samples of the total community (Peet, 1974).

Evenness of spread $E = H'/H'_{\max}$, where $H'_{\max}$ is $\log_2$ (no. of species). Niche breadth, based on microhabitats occupied, or food taken, or times of activity, was calculated from Simpson's index of diversity

$$B = \frac{1}{\sum_{i}^{n} p_i^2}$$

where p_i represents the proportion of the ith microhabitat (or food resource, or time period) actually used; B varies from unity to n depending on the p_i values, and is standardized by dividing by n. For calculating habitat-niche breadth values, and following Krebs and Wingate (1976), data were converted to captures/100 trapnights/trap station, thus B = niche breadth, p_i = proportion of species' total density in microhabitat (=trap station) $_i p$ is defined from average density estimates:

$$p_i = \frac{d_i}{\Sigma d_i}$$

where d_i = number of individuals per 100 trapnights in microhabitat i. Standardized niche breadth for each species in any of the four habitats was then obtained by dividing by n, or the number of trap stations.

Habitat-niche breadth and overlap (see below) was calculated for each of the four habitats separately, and then for the whole transect.

Niche overlap between any two species, for a given niche dimension, was calculated following Pianka (1973):

$$O_{ij} = O_{ji} = \frac{\Sigma(X_{ik}\ X_{jk})}{\sqrt{\Sigma X_{ik}^2\ \Sigma X_{jk}^2}}$$

where $O_{ij} = O_{ji}$ = niche overlap between species i and species j (range 0–1)

X_{ik} = proportion of species i numbers in resource k (microhabitat, food type, time period)

X_{jk} = proportion of species j numbers in resource k.

RESULTS

Table 1 lists the species present in the study area. Owing to the sampling technique some species were not collected in the regular trapline. For example, most of the *Acacia erioloba* trees close to the trapline harbored tree rats *Thallomys paedulcus*, but they were virtually restricted to these "habitat is-

Table 1.—*Species of small mammals recorded in the study area 1970–1976. Approximate weight in grams, basic activity period, and relative density (no. captures/100 trapnights over 11 trapping periods in all four habitats) are given, as well as the habitats in which captured or seen. Abbreviation for habitats: LD = low dune; RB = riverbed; PL = plateau; HD = high dune.*

Taxa	Weight	Activity	Relative density	Habitats
Order Insectivora				
Family Macroscelididae				
Elephantulus intufi	51.4	diurnal	0.13	LD, RB, HD
Family Soricidae				
Crocidura hirta	16.0	nocturnal	0.01	LD
Order Rodentia				
Family Sciuridae				
Xerus inauris		diurnal		RB
Family Pedetidae				
Pedetes capensis		nocturnal		LD, RB
Family Cricetidae and Muridae				
Subfamily Gerbillinae				
Gerbillurus paeba	25.9	nocturnal	3.31	All
Desmodillus auricularis	46.1	nocturnal	0.37	All
Tatera brantsii	64.9	nocturnal	0.37	LD, PL, HD
Subfamily Otomyinae				
Parotomys brantsii	80.0	diurnal		LD
Subfamily Dendromurinae				
Dendromus melanotis	6.3	nocturnal	0.08	LD, PL, HD
Malacothrix typica	13.0	nocturnal	0.01	PL
Subfamily Murinae				
Rhabdomys pumilio	32.0	diurnal	4.68	All
Mus minutoides	4.7	crepuscular/diurnal	0.37	All
Aethomys namaquensis	42.6	nocturnal	0.01	LD
Zelotomys woosnami	62.4	nocturnal	0.08	LD, HD
Thallomys paedulcus	75.0	crepuscular/nocturnal		LD, RB
Saccostomus campestris	47.0	nocturnal	0.04	PL, HD
Family Bathyergidae				
Cryptomys hottentotus		?		LD
Family Hystricidae				
Hystrix africae-australis		nocturnal		LD

Table 2.—*Relative density (no. of captures/100 trapnights) of small mammals in each of four habitats in the Nossob River, Kalahari Gemsbok National Park.*

Habitat	Census period										
	December 1970	May 1971	January 1972	July 1972	January 1973	January 1974	July 1974	December 1974	July 1975	January 1976	July 1976
Low dune	2.38	1.91	21.91	38.57	—	6.19	30.00	8.57	8.57	3.33	26.67
Riverbed	1.06	7.41	15.34	25.93	1.05	2.12	25.40	8.47	3.70	2.12	14.29
Plateau	0.43	—	4.76	24.24	—	0.43	9.09	—	0.43	0.87	7.36
High Dune	2.04	2.04	14.97	43.54	0.68	11.57	19.05	6.80	6.80	5.44	13.61
Overall	1.42	2.70	13.90	32.10	0.39	4.51	20.60	5.70	4.63	2.70	15.44

lands" and are therefore not reflected in the captures. Similarly, although the trapline bisected a large *Parotomys brantsi* colony during 1972, none were collected, probably due to the type of trap utilized (Nel and Rautenbach, 1976). On occasion small groups of ground squirrels crossed the census area, as did *Pedetes capensis*, but again they were not trapped. Otherwise the three trap-types used proved effective for collecting the other species present.

Fig. 1 shows that over the 6-year period December 1970 to December 1976 the total number of small mammals, as well as the number of and contribution by different species, fluctuated a great deal. Total numbers showed three peaks and three troughs, which relate fairly closely to rainfall during the previous 12 months. The low number of captures (5) in December 1976, after the study area was accidentally completely burned 6 weeks previously, obviously cannot be used for comparative purposes.

Between-habitat Variation

Although the study area was arbitrarily divided into four habitats on the grounds of differing vegetational aspects and soil types, pronounced differences were apparent in the relative density of small mammals in each habitat, and therefore its contribution to total numbers (Table 2). The plateau always had the lowest relative density, and contributed least to the community sampled by the transect. Otherwise either the low dune or high dune habitat usually had the highest relative density and contributed most. In brief, an equal or nearly equal amount of rainfall has a different effect on the productivity of the different habitats, and their ability to support different species.

The species diversity (using the Shannon-Wiener index) was usually higher in the low and high dune than in the riverbed and plateau, but marked dominance by one species often resulted in very unequal distribution of total numbers among species, which resulted in a decrease of evenness in spread or *E* (Table 3). However, as the number of species (and therefore diversity) increased, in most cases, especially in the low and high dune habitats, an increase in evenness of numerical distribution between species resulted. Sometimes, however, notably from January to July 1976 in the high dune habitat, diversity remained virtually constant but evenness decreased markedly.

Changes in Community Structure and Numbers

Apart from the changes in relative density of animals in each of the four habitats, changes also oc-

Table 3.—*Changes in species diversity of small mammals of four habitats in the Kalahari Gemsbok National Park. For calculations of H' and E, see methods. * = insufficient data.*

Trapping period		Low dune	Riverbed	Plateau	High dune	Overall
January 1972	H'	0.97	0.79	0.68	0.70	1.41
	E	0.42	0.50	0.68	0.44	0.50
July 1972	H'	1.97	1.16	1.54	1.14	1.76
	E	0.76	0.58	0.55	0.49	0.59
January 1974	H'	1.88	*	*	*	*
	E	0.81	*	*	*	*
July 1974	H'	1.89	0.25	1.41	1.98	1.69
	E	0.63	0.25	0.61	0.77	0.51
December 1974	H'	0.94	*	*	1.49	1.09
	E	0.60	*	*	0.94	0.54
January 1976	H'	1.38	*	*	1.41	1.49
	E	0.87	*	*	0.89	0.75
July 1976	H'	1.38	0.73	0.52	2.09	1.38
	E	0.53	0.46	0.52	0.81	0.49

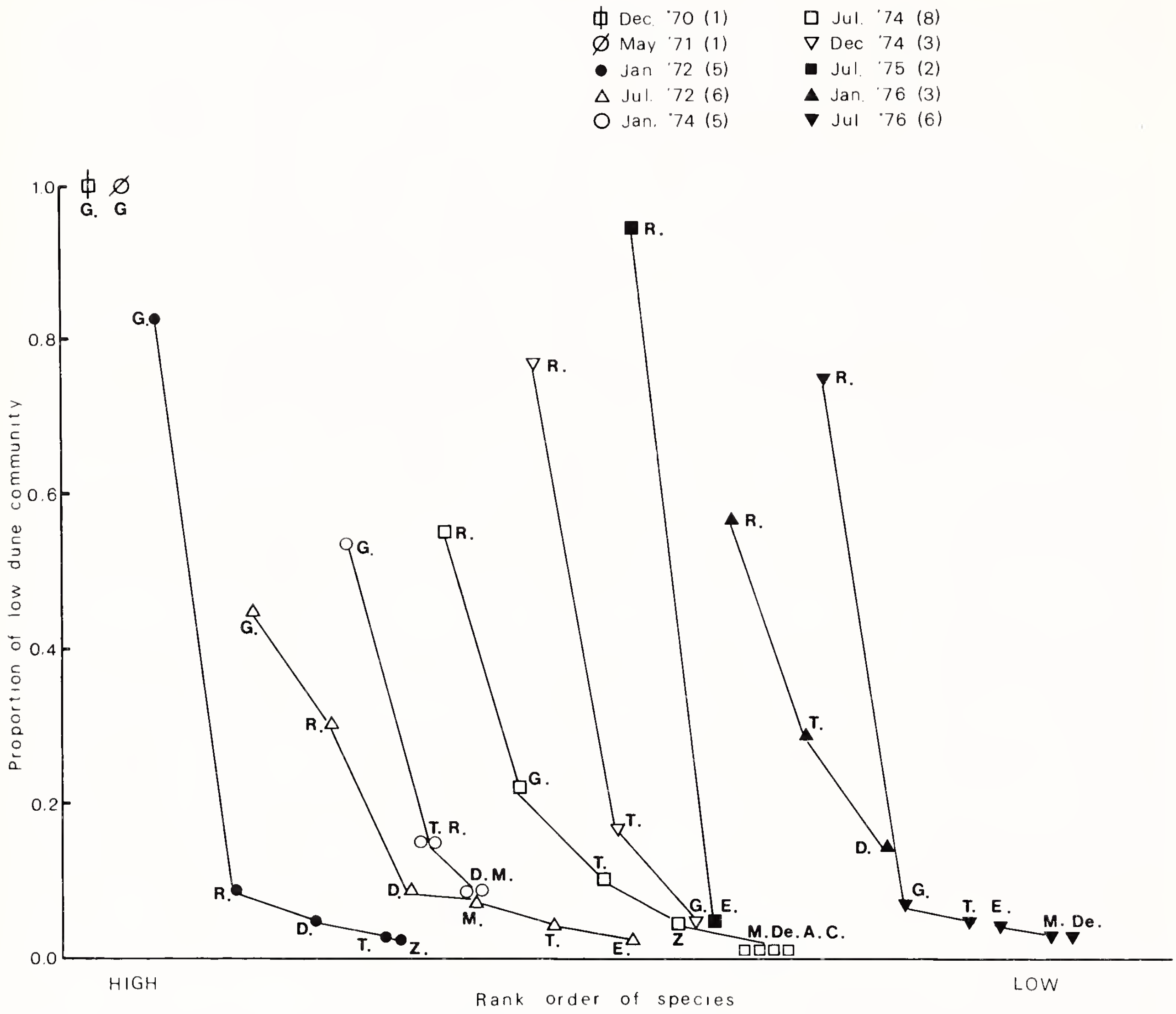

Fig. 2.—Contribution by different species to total numbers trapped at various times in the low dune habitat. Spacing of rank order of species, on horizontal axis, is arbitrary. G = *Gerbillurus paeba;* R = *Rhabdomys pumilio;* D = *Desmodillus auricularis;* T = *Tatera brantsii*; Z = *Zelotomys woosnami*; M = *Mus minutoides*; E = *Elephantulus intufi*; A = *Aethomys namaquensis*; De = *Dendromus melanotis;* C = *Crocidura hirta.*

curred in the proportion, which different species contributed to the community in a particular habitat at different periods (Figs. 2–4). On the low and high dunes, even though the number of species and the contribution by each in the community varied, the basic structure of the community remained very similar during the study period (Figs. 2 and 4). However, in the low dune community the proportions of total numbers contributed by the first and second ranking (in order of contribution) species were more fluid than in the high dune community. Over the study period, although the first or highest ranking species usually contributed a very large proportion to total numbers in either the low or high dunes, and thus dominated the particular community, this dominant species was not always the same. Figs. 2 and 4 also show that the period during which a particular species remained dominant was different in the low dune and high dune communities; in the former, *Gerbillurus paeba* was dominant up to January 1972, then again from December 1974 to July 1975, and again in July 1976, whereas *G. paeba* remained dominant in the high dune community up to January 1974.

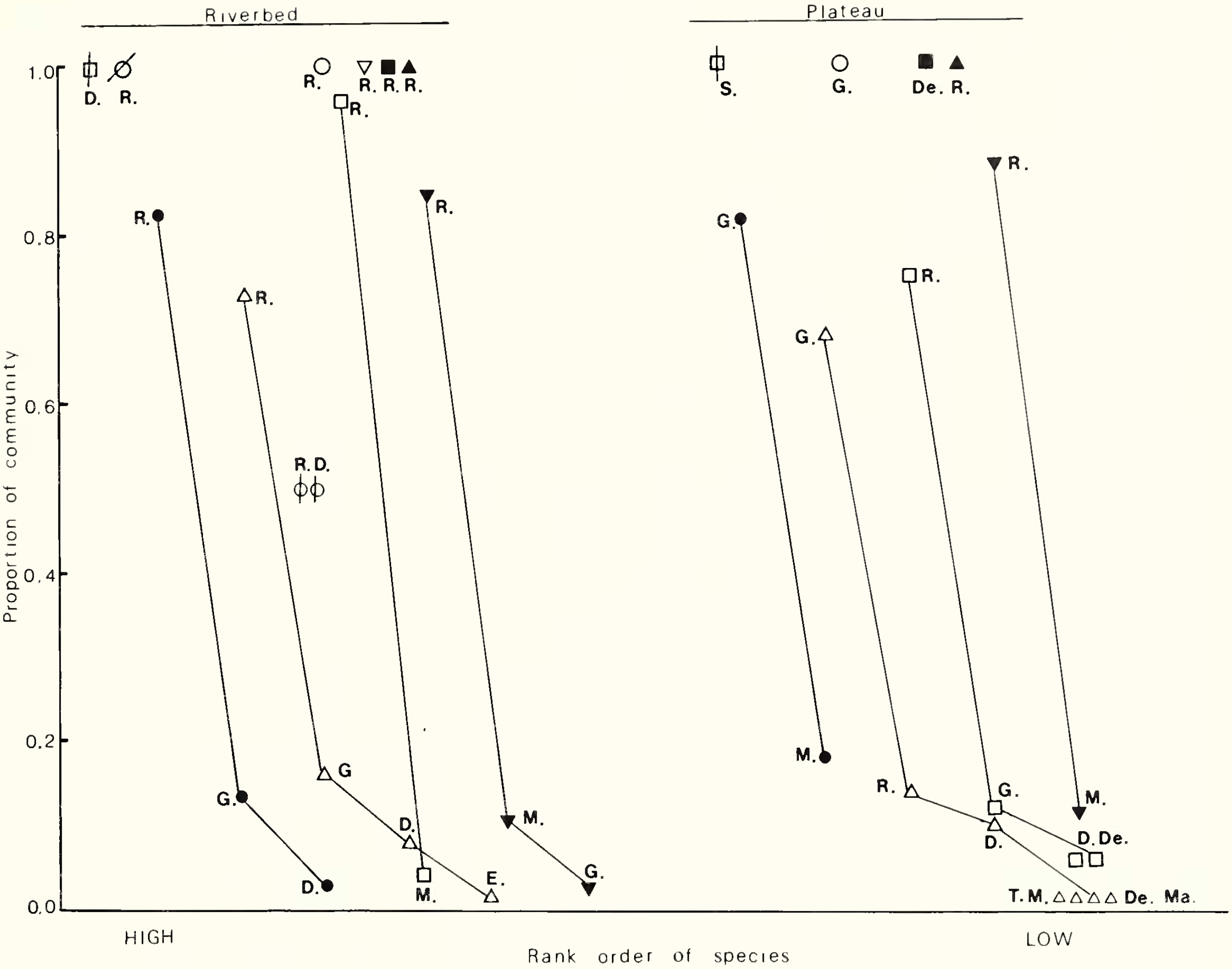

Fig. 3.—Contribution by different species, arranged in order of rank, to the riverbed and plateau communities. Ma = *Malacothrix typica;* S = *Saccostomus campestris.* Other abbreviations and symbols as in Fig. 2.

By contrast the communities in the riverbed and plateau showed a different structure. During most census periods the first-ranking species contributed nearly all the animals caught, and therefore completely dominated the community; also species diversity usually remained low (Table 3) and at times only one species was present.

It is of interest to note that the communities in the low and high dunes and riverbed (and on occasion the plateau) were primarily composed of species in the middle range of weight classes. When species numbers rose, it was the scarcer species at the bottom or top of the weight range that appeared. The selective factors mitigating in favor of a weight of 20 to 40 g in this particular environment remains, however, obscure.

Resource Utilization—Niche Dimensions

In this study, data were accumulated on only three facets of each species' niche, so that resource partitioning can only be attempted on the spatial, trophic, and temporal (or habitat, food, and time of activity) levels. As the traps were placed on the ground only indirect assessment of vertical activity or foraging levels can be attempted. Also no quantitative data are available for those species present in the study area but not trapped (see Table 1, and above).

Vertical feeding levels are shown in Fig. 5, but no quantitative data are available to allow differential utilization of various feeding levels to be assessed. Horizontal distribution is somewhat better documented, and standardized habitat-niche

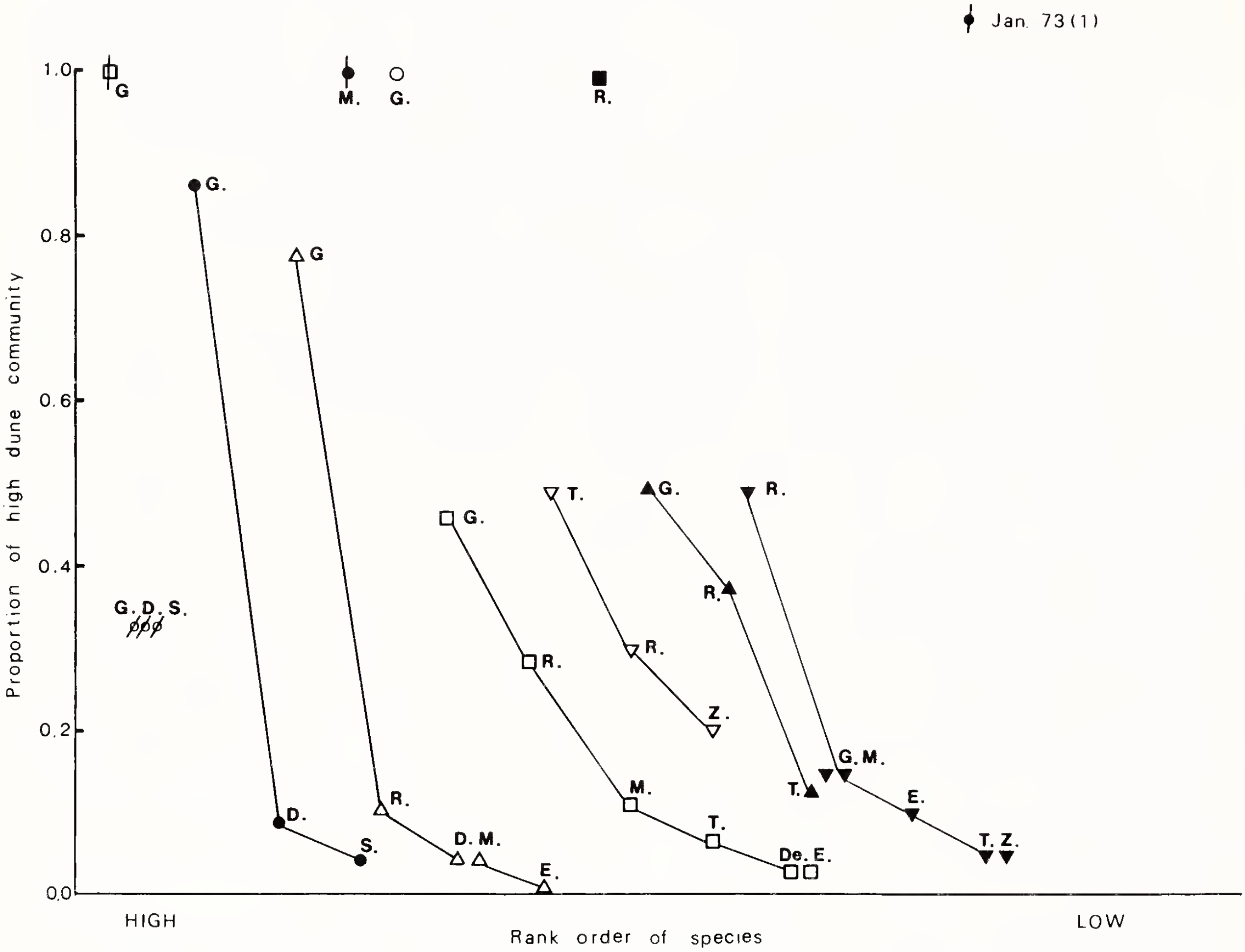

Fig. 4.—Contribution by different species, arranged in rank order, to total numbers trapped at various times in the high dune habitat. Abbreviations and symbols as in Figs. 2 and 3.

breadths, calculated as described in the methods section, are given in Table 4. As predicted by Levine (1968), niche breadth tends to increase to an asymptote as numbers rise (Fig. 6 and Table 4). As is to be expected, the more common species at any level of total number of animals or species present, for example, *G. paeba* and *R. pumilio,* tend to have wider habitat-niche breadth (Table 4), which indicates that they are less specialized and were utilizing the available habitat to a greater degree than others. The limiting factors in the habitat for any species remain conjectural, but subjectively cover seems to play a decisive role for at least some species; for example, *Desmodillus* favors very open and exposed areas, relying on acute hearing for perceiving predators (Lay, 1972), and, when rainfall and vegetative cover increases, as happened after 1972, they tend to decrease in numbers, being found in the general area only on places artificially cleared, such as campsites. Similarly, cover, in the broad sense, affected *Rhabdomys* abundance, whereas *Thallomys,* being here confined to large camelthorn *Acacia erioloba* trees, had a very patchy distribution but probably reasonably stable numbers.

The amount of habitat-niche overlap, calculated as explained in the methods section, among the more common species at the higher levels of abundance (see also Table 2) are given in Tables 5 and 6. During periods of low numbers, species do not overlap in the habitats and/or microhabitats (distribution points) utilized. For example, in December 1970 *Gerbillurus* occurred only on the low and high dunes, *Desmodillus* in the riverbed, and *Saccostomus* on the plateau; in May 1971, *Gerbillurus* again occurred only on the low and high dunes, *Rhab-*

Table 4.—*Standardized habitat niche breadth of five rodent genera trapped at 37 trap stations in four habitat types in the Nossob River, Kalahari Gemsbok National Park, from December 1970 to July 1976. LD = low dune, RB = riverbed, Pl = plateau, HD = high dune. Overall values are for transect as a whole. (—) Denotes absent from a particular habitat type during that trap session.*

		Trap session										
Taxa	Habitat	December 1970	May 1971	January 1972	July 1972	January 1973	January 1974	July 1974	December 1974	July 1975	January 1976	July 1976
Gerbillurus	LD	0.36	0.16	0.80	0.75	—	0.54	0.65	0.10	—	—	0.20
	RB	—	—	0.30	0.44	—	—	—	—	—	—	0.11
	Pl	—	—	0.49	0.71	—	0.09	0.18	—	—	—	—
	HD	0.26	0.14	0.69	0.88	—	0.64	0.78	—	—	0.38	0.14
	Overall	0.14	0.06	0.48	0.60	—	0.23	0.36	0.03	—	0.07	0.10
Desmodillus	LD	—	—	0.20	0.45	—	0.10	—	—	—	0.10	—
	RB	0.22	—	0.11	0.30	0.11	—	—	—	—	—	—
	Pl	—	—	—	0.33	—	—	0.09	—	—	—	—
	HD	—	0.14	0.14	0.43	—	—	—	—	—	—	—
	Overall	0.05	0.03	0.10	0.36	0.03	0.03	0.03	—	—	0.03	—
Tatera	LD	—	—	0.10	0.27	—	0.20	0.23	0.18	—	0.10	0.10
	RB	—	—	—	—	—	—	—	—	—	—	—
	Pl	—	—	—	0.09	—	—	—	—	—	—	—
	HD	—	—	—	—	—	—	0.29	0.40	—	0.14	0.14
	Overall	—	—	0.03	0.10	—	0.05	0.10	0.12	—	0.05	0.04
Rhabdomys	LD	—	—	0.27	0.57	—	0.20	0.73	0.65	0.57	0.27	0.87
	RB	—	0.42	0.50	0.77	0.11	0.30	0.84	0.43	0.26	0.30	0.53
	Pl	—	—	—	0.32	—	—	0.37	—	—	0.09	0.22
	HD	—	—	—	0.47	—	—	0.68	0.43	0.60	0.43	0.60
	Overall	—	0.10	0.16	0.47	0.03	0.12	0.57	0.30	0.33	0.24	0.51
Mus	LD	—	—	—	0.36	—	0.10	0.10	—	—	—	0.20
	RB	—	—	—	—	—	—	0.22	—	—	—	0.33
	Pl	—	—	0.18	0.09	—	—	0.09	—	—	—	0.18
	HD	—	—	—	0.43	0.14	—	0.26	—	—	—	0.26
	Overall	—	—	0.05	0.19	0.03	0.03	0.11	—	—	—	0.23

domys only in the riverbed, and *Desmodillus* and *Saccostomus* on the high dune, but not at the same distribution (= trapping) points.

During January 1974, *Gerbillurus*, *Tatera*, *Rhabdomys*, *Desmodillus*, and *Mus* occurred on the low dune; in the riverbed only *Rhabdomys* occurred and on the plateau and high dune only *Gerbillurus*. Overlap values for the low dune are as follows: *Gerbillurus*/*Tatera* = 0.24; *Gerbillurus*/*Rhabdomys* = 0.24; *Gerbillurus*/*Mus* = 0.33; *Gerbillurus*/*Desmodillus* = 0.33; *Rhabdomys*/*Tatera* = 0.50. Otherwise, the species present did not overlap in distribution points.

During December 1974, the only overlap was between *Gerbillurus* and *Rhabdomys* on the low dune (0.18), *Tatera* and *Rhabdomys* on the low dune and high dune (0.16 and 0.58, respectively), as well as *Tatera* and *Zelotomys* (0.67) and *Rhabdomys* and *Zelotomys* (0.58) on the high dune.

Few small mammals (apart from *Rhabdomys* only one each of *Dendromus* and *Elephantulus*) were captured in July 1975, and no overlap occurred.

In January 1976, there was overlap between *Tatera* and *Rhabdomys* only on the low and high dunes (0.41 and 0.58, respectively), *Tatera* and *Desmodillus* (1.0) and *Rhabdomys* and *Desmodillus* (0.41) on the low dune, and between *Gerbillurus* and *Rhabdomys* (0.24) and *Tatera* and *Rhabdomys* (0.58) on the high dune.

To relate amount of habitat-niche overlap to any degree of competition among species would probably be fallacious. Obviously, a high amount of overlap between *Rhabdomys* (diurnal) and *Gerbillurus* (nocturnal) may not be competition for the same resource, as this is used at different times. Probably the same applies as well to all nocturnal species, which may utilize the same place, but at different times of the night. Where a high amount

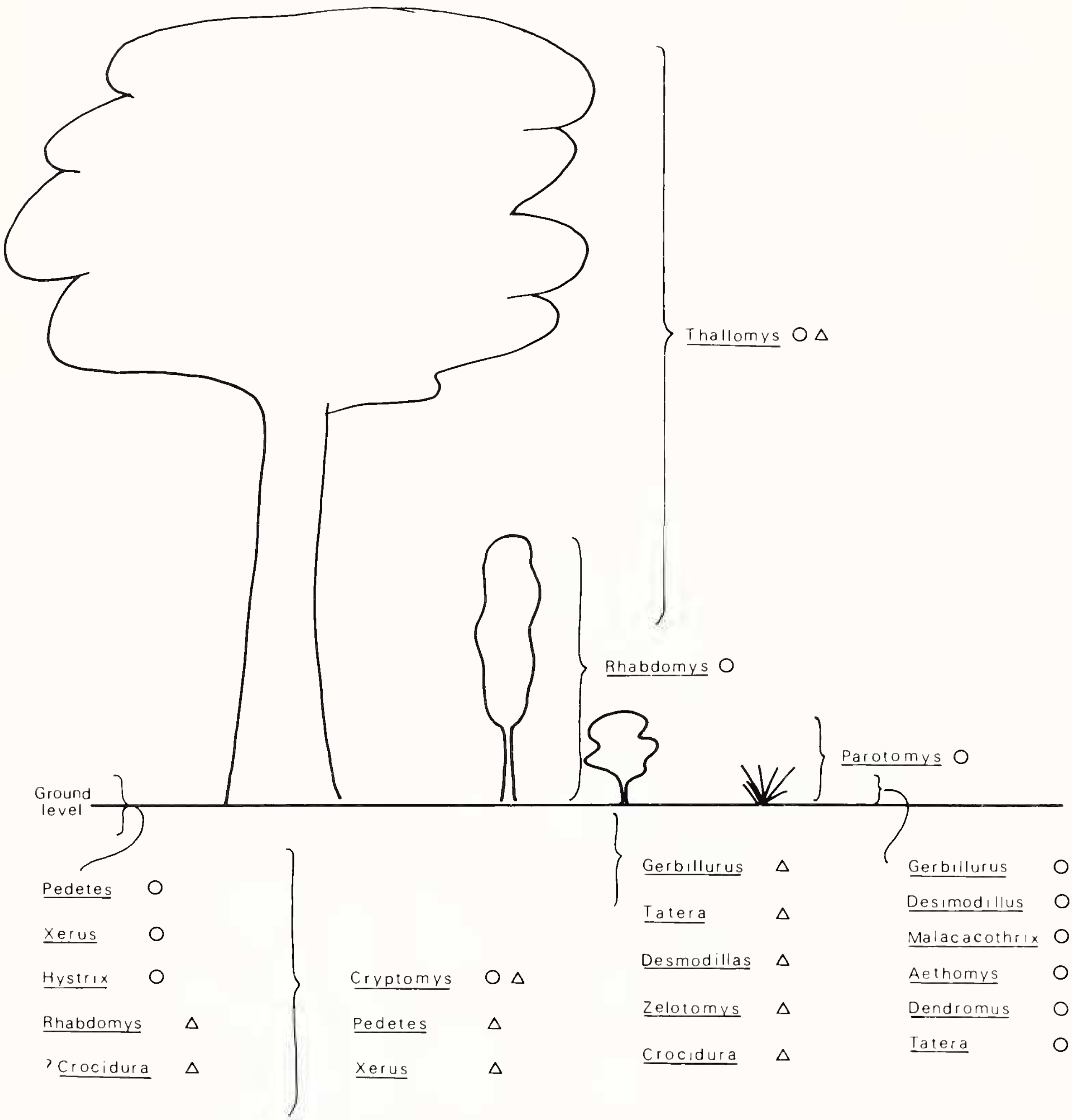

Fig. 5.—Vertical foraging levels (open circles), or level at which nesting sites occur (open triangles). Not drawn to scale.

of spatial overlap does exist (see Tables 5 and 6), different food sources in the same general area may well be utilized (Table 7). Niche overlap is perhaps better seen as an indication of the similarity of habitat (or microhabitat) favored by different species, and unless numbers reach critical heights and competitive exclusion can be demonstrated, available space should never be at a premium. In the absence of quantitative data on plant distribution, or occurrence of areas of different foliage height diversity, however, it must remain an open question whether availability of different grades (or degrees) of cover might turn out to be a limiting factor for some species, in the presence of others.

Table 5.—*Habitat niche overlap of five rodent genera based on occurrence at 37 microhabitats (trap stations) in the Nossob River, Kalahari Gemsbok National Park. Values above the bold face numbers are July 1972 data*, below are January 1972 data. Single figures refer to overall overlap; columns—top figure is overlap on low dune, then overlap on riverbed, plateau, and high dune (bottom figure) 0.00 denotes that species occur together in same habitat, but do not overlap at trapping points; — species do no co-occur in same habitat.*

Taxa	*Gerbillurus*		*Desmodillus*		*Tatera*		*Rhabdomys*		*Mus*	
Gerbillurus	**1.00**		0.44	.45 .51 .49 .60	0.13	.24 — .15 —	0.33	.55 .47 .57 .45	0.40	.47 — .59 .40
Desmodillus	0.23	.53 .00 — .00	**1.00**		0.21	.12 — .63 —	0.38	.49 .36 .52 .30	0.39	.57 — .32 .33
Tatera	0.12	.15 — — —	0.00	.00 — — —	**1.00**		0.33	.63 — .00 —	0.30	.39 — .00 —
Rhabdomys	0.10	.49 .14 — —	0.10	.00 .27 — —	0.00	.00 — — —	**1.00**		0.31	.45 — .00 .45
Mus	0.04	— — .18 —	0.00	— — — —	0.00	— — — —	0.00	— — — —	**1.00**	

* Other overlap values for July 1972 are *Rhabdomys/Elephantulus* = 0.30 .14 .58 — .26; *Dendromus/Gerbillurus* on plateau only—.22, or 0.11 overall; *Malacothrix/Gerbillurus* on plateau only—.30, or 0.14 overall.

Food

The food taken by the different species is given in Table 7; based on the three food-type categories, the standardized food-niche breadths are given in Table 8, and food-niche overlap in Table 9. As only three food categories were possible, data for food niche breadth and overlap should be viewed with caution, as these only reflect use *among* categories, and not *within* categories, which would perhaps be far more meaningful. These reservations of course apply equally to the figures for food-niche overlap. Nevertheless, as can be seen from Table 8, the niche breadth for most species increased during summer, when more insects were generally taken (Table 7). The very high niche overlap values (Table 9) between the majority of species probably reflects an artifact due to the low number of food categories and is thus probably more apparent than real. As the overlap values are lower in summer than winter, however, it could suggest that competition for food might become a factor in the latter season.

Time Activity

Limited data on activity cycles are available for only three species (*G. paeba, D. auricularis,* and *T. brantsii*). Based on this, temporal niche breadths are as follows: *G. paeba,* B = 0.89 (14 h activity); *D. auricularis,* B = 0.95 (14 h activity); and *T. brantsii,* B = 0.94 (13 h activity). Temporal niche overlap values are *Gerbillurus/Desmodillus* = 0.94; *Gerbillurus/Tatera* = 0.87; and *Desmodillus/Tatera* = 0.95. As these activity cycles were obtained in the laboratory it is arguable how well they relate to field conditions.

CONCLUSIONS

In general it was found that the number of species present closely followed the trend in total number of animals, and that the leaf-eating species, as one would expect, reacted more quickly to increased

Table 6.—*Habitat niche overlap values of six rodent genera based on occurrence at 37 microhabitats, in the Nossob River, Kalahari Gemsbok National Park. Values above the boldface numbers are for July 1974 data, below are July 1976* data. For other explanations, see legend to Table 5.*

Taxa	*Gerbillurus*		*Tatera*		*Rhabdomys*		*Mus*		*Zelotomys*		*Dendromus*	
Gerbillurus	**1.00**		0.50	.64 — — .38	0.35	.55 — .64 .74	0.22	.00 — — .48	0.45	.65 — — —	0.29	.37 — .00 .36
Tatera	0.00	.00 — — .00	**1.00**		0.06	.10 — — .00	0.06	.00 — — .32	0.37	.39 — — —	0.24	.22 — — .71
Rhabdomys	0.23	.25 .66 — .20	0.20	.28 — — .20	**1.00**		0.27	.16 .38 .41 .43	0.16	.28 — — —	0.15	.16 — .54 .00
Mus	0.34	.50 .00 — .45	0.00	.00 — — .00	0.47	.25 .55 .73 .82	**1.00**		0.00	.00 — — —	0.17	.00 — — .45
Zelotomys	0.00	— — — .00	0.32	— — — 1.0	0.05	— — — .20	0.00	— — — .00	**1.00**		0.00	.00 — — —
Dendromus	0.33	.50 — — —	0.00	.00 — — —	0.27	.40 — — —	0.20	.50 — — —	—		**1.00**	

* In July 1976 *Elephantulus/Gerbillurus* overlap on low dune by 0.32; *Elephantulus/Rhabdomys* by 0.34 on low and 0.72 on high dune; and *Elephantulus/Mus* by 0.63 on the high dune.

rainfall than did the seedeaters. The discrepancy between the numbers of seedeaters in July 1972 and July 1974, in relation to rainfall, can be explained, albeit subjectively in the absence of quantitative data, by a marked increase in cover during 1974, which adversely affected the gerbils, in particular *G. paeba* and *D. auricularis*. The high numbers of small mammals during July 1972, compared to the rainfall, are more difficult to explain. However, two factors may account for this seeming anomaly—cloud cover, days of rainfall per month, temperature, and amount of precipitation per shower vary

Table 7.—*Percentage of diet composed of white plant material, green plant material, or insects, of eight genera of mammals in the Kalahari Gemsbok National Park.*

	Winter					Summer				
Taxa	No. seasons involved	N	% white	% green	% insects	No. seasons involved	N	% white	% green	% insects
Gerbillurus	2	11	76.4	23.6	0.0	3	43	39.3	43.8	16.8
Desmodillus	1	5	71.0	29.0	0.0	2	4	15.0	40.0	45.0
Tatera	3	12	67.1	27.5	5.4	3	22	34.5	59.9	5.6
Mus	2	10	81.0	2.0	17.0	1	1	100.0	0.0	0.0
Rhabdomys	2	62	31.0	58.0	11.0	2	5	18.0	72.0	10.0
Zelotomys	2	1		100% flesh		1	1	75.0	0.0	25.0
Dendromus	1	2	95.0	5.0	0.0				no data	
Elephantulus	1	3	8.3	0.0	91.6				no data	

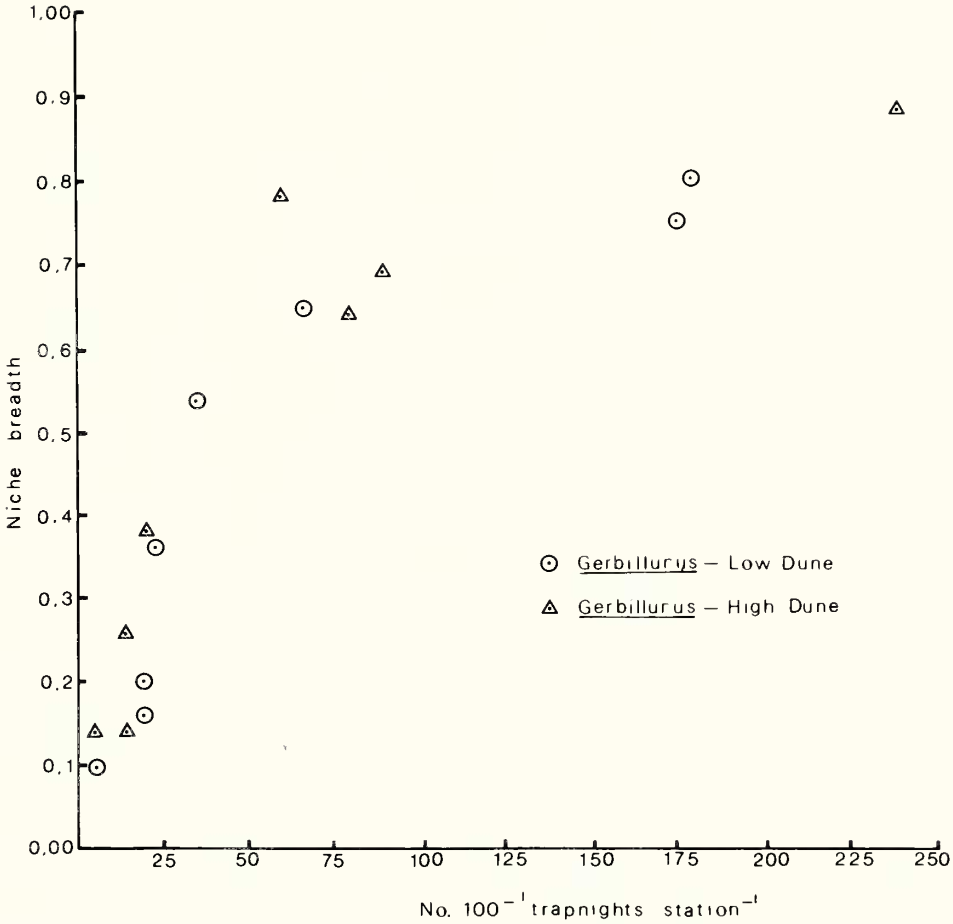

Fig. 6.—Standardized habitat niche breadth, based on 37 trapping stations of *Gerbillurus paeba* in the Nossob River, plotted against projected number of trapnights per station.

considerably and thus would affect evapotranspiration or effective rainfall, rather than actual rainfall as given here; and secondly, rainfall in the Kalahari is very patchy so that the measured rainfall during 1971–1972 may not have accurately reflected rainfall on the study area some 3 km distant.

Table 8.—*Standardized food-niche breadth of eight small mammal genera in the Kalahari Gemsbok National Park, based on percentage food taken of three categories—white plant material, green plant material, and insects. Sample size given in parentheses.*

Taxa	Winter		Summer	
Gerbillurus	(11)	0.52	(43)	0.89
Desmodillus	(5)	0.57	(4)	0.87
Tatera	(12)	0.63	(22)	0.69
Mus	(10)	0.49	(1)	0.33
Rhabdomys	(62)	0.75	(5)	0.59
Zelotomys	(1)	0.33	(1)	0.53
Dendromus	(2)	0.37	no data	
Elephantulus	(3)	0.39	no data	

As the transect extended for only 720 m, rainfall was probably fairly equal along its length. Even so, various parts of the study area seem to respond differently as far as small mammal species diversity and density are concerned, which justifies subdivi-

Table 9.—*Food-niche overlap values of six small mammal genera in the Kalahari Gemsbok National Park. Values above the boldface numbers are for winter, below are for summer.*

Taxa	*Gerbillurus*	*Desmodillus*	*Tatera*	*Rhabdomys*	*Mus*	*Elephantulus*
Gerbillurus	**1.00**	0.99	0.99	0.70	0.94	0.09
Desmodillus	0.82	**1.00**	0.99	0.76	0.92	0.08
Tatera	0.96	0.74	**1.00**	0.77	0.93	0.16
Rhabdomys	0.88	0.78	0.96	**1.00**	0.51	0.21
Mus	0.64	0.24	0.50	0.24	**1.00**	0.29
Elephantulus	—	—	—	—	—	**1.00**

sion of the area into four distinct habitats. Differences in soil types are perhaps primarily responsible for the variation not only in plant species present and therefore food resources, but perhaps more crucially different growth forms and thus the amount and degree of cover. This would affect not only the species able to survive in a given habitat, but also the numbers it can attain in each. Whether the differences between the low and high dune habitats are real and long-term, or a result of receiving slightly different rainfall, with the resultant effects on food and cover availability, is difficult to determine; certainly the same species was not always dominant in both (Figs. 2 and 4). Certainly the low and high dunes seem more favorable to most species than the other two habitats.

As has been found for other areas as well, the community in a particular habitat comprised only a few species (in a number of cases only one) contributing the majority of animals. There are thus one abundant, a few common, and rather more scarce species present in the community, especially of the low and high dunes. In comparison the riverbed and plateau had on most occasions a depauperate small mammal fauna. However, improved conditions due to increased rainfall not only elevate numbers of species usually present, but also provide the opportunity for other species to colonize the habitats, but at very low levels of density. Due to the sampling technique employed, no real idea of distribution patterns of these scarce species emerged, but they probably exist in widely separated pieces of optimal habitat and therefore have a patchy distribution. Conditions favoring the rapid increase in numbers of wide-ranging species, and by analogy those having a wide niche breadth in any resource axis, should also permit a wider distribution and higher numbers of the usually scarce species.

Although the number of species actually recorded on the transect is surprisingly high and diverse as far as taxonomic affinities and weight class distribution is concerned, not all exist in the same habitat at the same time. The numerically dominant *G. paeba* and *R. pumilio*, even were they to compete for the same food source, do so at different times; although *G. paeba* and *T. brantsii* overlap to a large extent in their food requirements, there is little overlap in activity time and even less in their use of the horizontal plane of the habitat.

Some species separate themselves rather completely in a vertical stratification of the habitat—for example, *Thallomys* has no competitors in the top layer of *Acacia* trees and only marginally overlaps with *Rhabdomys* closer to the ground, but at a different time of day; *Cryptomys*, being entirely fossorial, eliminates itself from competing with others effectively in this way.

The composition of the community in a particular habitat during a specific period most probably results from extrinsic factors such as rainfall, and the concomitant changes in the habitat rather than from any effects of competition between species for available resources. Viewed subjectively, increased cover favors some species (*Rhabdomys, Zelotomys, Aethomys, Crocidura*) while depressing numbers of others, for example *Gerbillurus* and *Desmodillus*. It is therefore clear that the composition of the small mammal community in the study area as a whole, or in particular habitats, was fluid during the study period. Presence or absence of a species probably resulted from the degree of adaptation of species to prevailing conditions.

To use the limited data available as a basis for describing the niches occupied by the various species would be rather naive. However, the data do give some idea of resource utilization by each species, though because some species were present in such low numbers results for them must remain tentative. The data do show that the species usually present, or those being more abundant, have wider niche dimensions than the scarcer or only sometimes present ones. This agrees with current ideas of niche dimensions (Pianka, 1976). The four habitats recognized (low dune, riverbed, plateau, high dune) differ in substrate composition, degree and diversity of plant cover, and to some extent slope and therefore (based on limited data available) temperature and humidity regimes. These differences affect the probablity of species occurring in each habitat, and the numbers they can attain. Apart from these spatial differences, temporal changes in the habitat are brought about by variation in rainfall, but increased (or decreased) rainfall does not affect all habitats equally.

The two most common species, *G. paeba* and *R. pumilio*, are separated in the first place by their activity cycles, being nocturnal and primarily diurnal, respectively. There is also a good separation as far as the habitat is concerned, with *G. paeba* being common on the low and high dunes (patchy vegetative cover) and *R. pumilio* being more common in the riverbed, which has a dense grass cover. Increased cover, due to rainfall, restricts the occurrence of *G. paeba*, no matter which habitat is looked at, with the reverse being true for *R. pumilio*. Diet-wise these two species are also widely separated with *G. paeba* selecting seeds in winter, but favoring green plant material and insects in summer (perhaps to offset increased evaporative loss due to higher ambient temperatures, even at night), and with *R. pumilio* being primarily a grass-eater year-round. Therefore, wherever cover is sufficiently patchy, and soil type amenable to digging, *G. paeba* occurs, whereas *R. pumilio* is totally dependent on good cover to avoid predators (see also Nel, 1975).

The two other gerbils, *D. auricularis* and *T. brantsii*, are both nocturnal, with a high amount of activity overlap between them and also with *G. paeba*. Both occur on sandy soil, but in the case of *D. auricularis* this must be firm and with very low plant cover. Although the amount of overlap in basic food resource (seeds) among the three gerbils is high, this may be more apparent than real, because of the coarse division of food and the absence of separation into seed-sizes (different-sized seeds perhaps being taken by the different-sized gerbils, as found also by Brown and Lieberman, 1973). Although low habitat-niche overlap values were recorded between *G. paeba* and *T. brantsii*, subjective assessment of the presence of *Gerbillurus* and *Tatera* burrows would indicate a much greater spatial overlap between these two genera. In the absence of quantitative data, it is difficult to say whether there is any "avoidance" effect between them when foraging, or whether trap placement (inside, at edge, or away in open from bushes) is responsible (see Brown, 1975). The only other species caught in some numbers, *Mus minutoides*, shows some spatial overlap with *Gerbillurus*, *Desmodillus*, *Tatera*, and *Rhabdomys*, but only so when total numbers of small mammals are high. In summer little food niche overlap occurs among *M. minutoides* and the others, but in winter this rises to appreciable figures. However, the very small size of *M. minutoides* probably results in very small seeds being taken, lessening competition for food with the others. The time of activity (crepuscular, diurnal) would tend to separate *Mus* from most other species apart from *R. pumilio*.

The precise factors shaping the destinies of the communities and the niche dimensions of the various species must therefore still remain conjectural at present. The data accumulated do show, however, that in an arid area such as the Kalahari, community structure and niche dimensions are plastic and constantly changing. Future work will aim at trying to explain the reasons behind this phenomenon.

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NOTES ON THE FOOD AND FORAGING BEHAVIOR OF THE BAT-EARED FOX, *OTOCYON MEGALOTIS*

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ABSTRACT

Bat-eared foxes (*Otocyon megalotis*) were observed for about 180 h during 1976 and 1977 in the dry bed of the Nossob River, Kalahari Gemsbok National Park, South Africa. Observations were primarily directed toward obtaining data on the food eaten, foraging range, speed of foraging, time spent foraging, and interactions while foraging. Scats were also gathered and their contents were analyzed for species included and their percentage of occurrence. In general, invertebrates were selected as food items with termites predominating but food selection is opportunistic. Activity of foraging and feeding depends on the season; in winter the bat-eared foxes are chiefly diurnal, whereas in summer they are nocturnal. Preliminary data indicate that feeding bouts vary depending on the season. Home ranges overlap widely, with many groups often foraging in close proximity to one another.

INTRODUCTION

The bat-eared fox, *Otocyon megalotis*, is widespread in the drier regions of southern Africa, and recently seems to have been increasing its range (Smithers, 1971). Yet, apart from Bothma (1966, 1971) and Smithers (1971), little has been published on the food taken by this ubiquitous mammal.

METHODS

During February, July, and December 1976, and January 1977, different groups of foraging bat-eared foxes were observed in the dry bed of the Nossob River, Kalahari Gemsbok National Park, South Africa, and notes taken on food eaten, foraging range, speed of foraging, time spent foraging, and interactions while foraging. Scats were also collected at random or when following known individuals. Observations were from vehicles, with 7 × 42 binoculars, and occasionally aided at night by foglamps, but more usually moonlight sufficed. Detailed observations were made on a pair, with cubs, in December and January. Scats were softened in water and contents identified using a Wild stereomicroscope. Super 8-mm cine films were taken when light conditions permitted, and subsequently analyzed on a frame by frame basis.

This paper is based on limited data (approximately 180 h of observations) and should therefore be seen as an interim report from an ongoing study.

RESULTS

Food

The different food items utilized by the foxes are given in Table 1; these are from detailed analyses of samples taken from various scats. For frequency of occurrence and comparative purposes, only broad categories were used (Table 2). This table shows that in general invertebrates are selected, with the frequency of occurrence of them in scats probably reflecting availability in the areas where the scats were collected, but with termites (*Hodotermes mossambicus*) predominating. However, if the percentage contribution of various items to the total volume of the scats are taken into account, more marked differences appear. For example, although during the summer "dry" season termites constitute the bulk of scats (60 to 98%, usually >90%) from the riverbed, they form only 20 to 45% of the volume of scats from the plateau (Nossob), probably reflecting local differences in availability of these prey items due to edaphic factors. Likewise, in the "wet" season, although termites occur in most scats, their volumetric contribution falls, but the contribution by *Grewia flava*, a small berry, rises to >50%. In January 1977, marked differences were also found between the composition of the scats from the male and female of the pair intensively followed; the female's scats were composed of 40 to 50% *Grewia*, 30 to 46% termites, and some scorpions, whereas that of the male consisted of 85% termites and about 2% *Grewia*. This discrepancy probably results from the difference in feeding range of the sexes (see below) during this period. The one and admittedly small sample of scats from the duneveld surrounding the river seems to indi-

Table 1.—*Food items taken by bat-eared foxes in the southern Kalahari.*

Termites	Order Isoptera; Family Hodotermitidae; *Hodotermes mossambicus*
Ants	Order Hymenoptera; Subfamily Campinotinae; *Campenotus fulvopilosus* and *Campenotus* spp. Subfamily Mirmicinae
Beetles	Order Coleoptera Family Carabidae Family Tenebrionidae Family Scarabaeidae Family Melolonthidae
Sunspiders	Order Solifugae; Family Solifugidae; *Solpuga* spp.
Grasshoppers and crickets	Order Orthoptera Family Arcridiidae Family Gryllidae
Moths and cutting worms (=larval forms)	Order Lepidoptera Family Noctuidae
Millipedes	Order Myriapoda
Scorpions	Order Scorpionida

cate a somewhat different diet, again probably reflecting between-habitat differences in food availability.

In contrast to the findings of Bothma (1971) and Smithers (1971) very few vertebrate remains were found in the feces. It would appear therefore that termites form an important part of the diet of bat-eared foxes in the southwestern Kalahari, being taken throughout the year. In winter, however, ants form the bulk of the foxes' diet, whereas *Grewia* berries, available in the "wet" season, are particularly favored. Indeed the female, intensively ob-

Table 2.—*Occurrence of food items in bat-eared fox feces from the southern Kalahari. The number of samples is indicated below each date. Figures in parentheses are percentages.*

		Winter—Dry		Summer—Dry		Summer—"Wet"			
Food items		Riverbed Nossob July 1976 98	Dunes Nossob July 1976 7	Riverbed Nossob December 1976 94	Plateau Cubitje Quap December 1976 54	Riverbed Nossob Early January 1977 54	Riverbed Nossob Middle January 1977 30	Plateau Nossob Middle January 1976 32	Plateau Cubitje Quap Early January 1977 13
Invertebrate	Termites	76 (77.6)	7 (100)	94 (100)	54 (100)	54 (100)	29 (96.7)	32 (100)	13 (100)
	Ants	85 (86.7)		51 (54.3)	49 (90.7)	43 (79.6)	14 (46.7)	10 (31.3)	13 (100)
	Beetles	63 (64.3)	7 (100)	84 (89.4)	54 (100)	52 (96.3)	19 (63.3)	23 (76.7)	7 (53.9)
	Beetle larvae	2 (2.0)		21 (22.3)	53 (98.2)	27 (50.0)	16 (53.3)	15 (46.9)	8 (61.5)
	Sunspiders	1 (1.0)	7 (100)	8 (8.5)	6 (11.1)	6 (11.1)	3 (10.0)	5 (15.6)	6 (46.2)
	Grasshoppers	33 (33.7)	7 (100)	5 (5.3)	3 (5.6)	3 (5.6)	4 (13.3)	2 (6.3)	
	Moths/worms	17 (17.4)		7 (7.5)	13 (24.1)			1 (3.1)	
	Scorpions					1 (1.9)	2 (6.7)		1 (7.7)
	Millipedes				1 (1.9)		2 (6.7)		2 (15.4)
Vertebrate	Hair	26 (26.5)	7 (100)	14 (14.9)	3 (5.6)	1 (1.9)	5 (16.7)	2 (6.3)	
	Bones	9 (9.2)	7 (100)	7 (7.5)					
	Feathers	4 (4.1)		5 (5.3)					
Vegetable	Grass	90 (91.8)	7 (100)	93 (98.9)	54 (100)	54 (100)	26 (86.7)	32 (100)	13 (100)
	Seeds	74 (75.5)		9 (9.6)	8 (14.8)		4 (13.3)		
	Grewia flava					23 (42.6)	18 (60.0)		11 (84.6)

served, would (in January) head early each evening straight for some *Grewia* bushes, browse for a while, and then continue foraging.

Foraging Time, Speed and Area

Activity (mostly spent on foraging and feeding) varies through the year and is perhaps related to thermoregulation. In winter, bat-eared fox groups in the riverbed are active by day, from approximately 0600 h up to 2000 h with a peak in foraging from 1200 h to about 1700 h. All groups flushed at night were lying down and presumably sleeping. In midsummer (December–January) on the other hand, the activity cycle was reversed, with individuals active from about 2000 h to about 0830 h, and slightly later if the day was overcast. Occasionally individuals were seen active as late as 1045 h, but this is exceptional. Especially in the late afternoons (1700 h) individuals would occasionally venture from dens, forage desultorily with evident signs of overheating for periods up to 15 min, and then return either to shade or the den itself. By mid-February foraging starts at 1600 h, and continues until about 0900 h, so it would seem that seasons impose a gradual shift in the activity cycle one way or the other.

The difference in the time spent foraging by a male and female with cubs, during December and January, was marked. The female would suckle the young before commencing foraging, and would then forage constantly for about 9.5 to 10 h before returning to the den to suckle the young; during this time away from the den she might spend about 15 to 30 min resting or grooming. After suckling the young in the morning she would forage for another 1 to 2 h, usually close to the den. The male, by contrast, forages for 3 to 4 h, and always close to the den; when not foraging, he lies at the den entrance. When the young first start foraging the male would forage alone for an hour or so, from 2000 h onwards, return to the den and accompany the cubs for 1 or 2 foraging trips, with a total time of around 3 h (data for early January). It seems probable therefore that as the cubs grow the time spent foraging by the male would gradually increase as the cubs increase their own foraging and rely less on suckling. Although data is available from only three dens it seems probable that this trait is common to bat-eared foxes in this region—the male guards the young and initiates them into foraging. Apart from suckling the young, all the female's time is taken up foraging, imposed by the rigors of nursing and the necessity to obtain enough nourishment for herself.

No regurgitation of food for the pair-mate at the den or the cubs was ever witnessed, nor was any food caching observed.

Suckling time also seems to decrease as the cubs grow older—a pair of very small cubs suckled for 7 min at Grootkolk on 3 December 1976; at the specific den we observed constantly near Nossob camp suckling continued for 7 min on 12 December 1976, 4 min 24.5 s on 4 January 1977, and for 3 min 50 s on 6 January 1977. Whether suckling in the den by day occurs is unknown; certainly when the cubs are very small this is the rule. As they grow suckling, at least in the late afternoon and early morning, takes place at the entrance to the den with the female standing up, hind legs slightly splayed, while the cubs more or less hang from the nipples as they suckle. Suckling from at least two different nipples by an individual cub during a single feeding bout is common. Suckling, with the female lying down, was never observed; if the cubs were still very small and tried to suckle while the female was recumbent, she would get up and disappear down the den, followed by the cubs.

Limited data suggest that the foraging range is to some extent dependent on group size; a group of 10 individuals followed for 3 days in February ranged over 1.5 to 2 square km, whereas the female closely observed in December/January had a foraging range of <1.0 square km, with that of her mate considerably less. Foraging areas tend to shift slightly over time, and those of neighbouring groups overlap widely. No defense or marking of foraging areas was ever seen; by contrast, up to 15 individuals (from four groups) have been seen foraging close together in an area of less than 0.5 square km. Foraging "speed" varies greatly, obviously depending on food availability; during February 1976, for a group of 10, this varied between 0.5 to 1.2 km/h. The female already referred to above foraged about 0.5 to 2 km/h, and usually moved about 12 km per night during the course of her foraging.

Feeding Bouts

Observations indicated (see below) that when actually feeding the position of the ears changes, from being directed forward to being pulled back. The time-interval between the flipping back-flipping forward again was taken as the duration of a particular feeding bout. It was often not possible to see an animal actually chewing, especially at night or when

Table 3.—*Number and duration of feeding bouts of bat-eared foxes in the southern Kalahari.*

Season	Time	N	No. bouts/ 15 min	Mean duration (s)	Range (s)	Prey
Winter "Dry"	1500 h to 1700 h	7	81.5	7.6	1–46.0	Termites
Summer "Dry"	2000 h to 0415 h	9	50.6	7.1	1–58.1	Mainly termites
Summer "Wet"	2000 h to 0835 h	13	40.0	3.5	1–22.9	?

the mouth was obscured by vegetation, but the ears were always visible. Table 3 summarizes the limited data on number, duration, and range of duration of feeding bouts by bat-eared foxes at various periods and times of day. The only continuous recording of feeding in a particular animal was in December 1976 on a known female; for that particular night (6–7 December 1976) it appeared that after the initial intensive feeding a somewhat more slack period in feeding happens near midnight; during this time extensive self-grooming took place. Thereafter both the number and duration of feeding bouts increased, but not to the previous level. However, a great deal of variation in number and duration of feeding bouts at a particular time period, but on different days, occurs in the same animal.

Whether the decline in feeding bouts is related to increasingly less activity of prey items as the night progresses, in summer at any rate, is unknown. The known female did however show changes in the number of digging bouts/15 min through the night as follows: from 2000 to 2200 h on average 4.3 bouts/15 min were performed; from 2200 to 0500 h none at all; thereafter the incidence of digging increased sharply up to about 9 bouts/15 min after 0800 h. The male tended to have more digging bouts, perhaps necessitated by his small foraging range during the time cubs were at their den.

Foraging Behavior

When leaving the den to forage, bat-eared foxes would do so without any preliminary scouting around for possible predators. Before setting off as a group, some members may indulge in bouts of allogrooming, and this was usually the case between the male and three cubs referred to above. Large groups tend to split up into smaller groups (often pairs) during the course of their foraging, and such subgroups may be separated by up to 200 m, although they move in the same general direction. Whether the composition of these subgroups remains constant is not known. Small family groups (two to five individuals) normally stay within five to 10 m of each other, often feeding close (<1 m) together.

The initial part of a foraging route can remain constant for a few days at a time, and this portion usually contains several deposits of feces added to every day. This may relate to wind direction; movement from the den is normally first downwind, and then for long distances (up to 1 km) crosswind. During foraging, movements tend to be erratic; straight-line movements between feeding stations of up to 50 m or more are interspersed with S-shaped runs, the latter especially evident when moving up- or downwind. When feeding stations are close together, movement is slow with frequent casting about, with often just the head and forequarters being moved as prey is taken first in front, then on the left or right side of the animal; complete turns can then occur. The fox's head is then seldom lifted, the nose remaining close to the ground surface. Movement, although in a general direction, tends to be erratic with frequent twists and turns.

When foraging, the head is held low and the ears pointed forward at about 45°. If the fox had been walking fast or running, the food source may be overshot, and, as the animal turns, the head is lowered abruptly. Otherwise the head is simply lowered even further. In all cases, when the prey is captured, the ears flip back from their front-facing position, and immediately as chewing or swallowing starts the ears point forward again. Sometimes the head is lifted when chewing or swallowing, but this is not the rule. Usually, after a few paces with the head held close to the ground and ears cocked forward, the head is lifted, back straightens, and the animal looks sideways.

On occasion, when moving at a run from one feeding station to the next, the impression is gained that the new prey source was first either heard or smelled, and then reacted to, or else it could be a known source of high prey (termites in all cases investigated) density. Certainly the movement seems purposeful, and serves to attract partner(s) to the same spot.

Perhaps due to the high density of termites in the study area little digging, or signs of it, was seen. Although bat-eared foxes are said to take birds, I observed no interest by foxes in birds flushed or alighting near them. On the other hand, grasshoppers or even moths are actively pursued, and foxes jump into the air to catch them. The "pounce" common to other canids, for example black-backed jackal, was seen only once in a pair foraging around a grass-covered fallen tree stump. Such patches of habitat normally contain numbers of striped mice, *Rhabdomys pumilio,* and these could have been the quarry of the foraging foxes. A more attenuated form of the pounce is seen when sunspiders are chased.

Little strife was ever noticed between pair or group members during foraging. Cubs are seldom snapped at by adults when foraging together, and this only happens when a cub would try to take a morsel away from the adult. Only on one occasion was frequent agonistic behavior seen between members of a pair; the prey items could not be identified with certainty (perhaps grasshoppers or beetles) and, while they were foraging with noses close together, one snapped at the other when the latter tried to take its prey from it. These interactions lasted about 1 to 2 s, with 12 occurring in 18 min.

DISCUSSION

The limited data available suggest that in the southwestern Kalahari bat-eared foxes subsist throughout the year almost exclusively on invertebrate prey. Although differences between the diets of individual bat-eared foxes are common, and depend to some extent on the particular habitat (for example, riverbed, plateau) occupied, seasonal trends in the diet of foxes in a particular habitat can be discerned. This results from changes in availability of prey items, and because the activity periods of the foxes shift with the changing seasons. In common with other canids, and probably also because of the rather stable home ranges, food selection is opportunistic. However, certain items are certainly preferred, especially the ripe berries of *Grewia flava,* if these occur in the home range of a particular fox. The bat-eared fox differs from other canids however in that food caching is absent—perhaps not unexpected, due to the nature of their prey.

The opportunistic nature of feeding would enhance social tolerance, as pointed out by Kleiman and Eisenberg (1973). Certainly the home ranges of bat-eared fox pairs, or groups, overlap widely and no defense of ranges was ever witnessed. In fact, many groups may forage in close proximity, utilizing the local abundance of particular prey items, such as termites. This is in contrast to the other two co-occurring canids, black-backed jackal, *Canis mesomelas,* and silver fox, *Vulpes chama,* in which mutually exclusive home ranges are found, and whose diets consist mainly of vertebrates, especially rodents. The foraging range of these canids overlaps and the diet of the bat-eared fox in the study area perhaps reflects an adaptation to food-niche separation, in order to lessen possible competition for the same resource.

The pair-bond in bat-eared foxes, common also to other canids (Kleiman and Eisenberg, 1973), is long lasting and the male plays a major role in guarding and rearing the young. The dispersed nature of the prey items, each with low individual nutritional value, forces the female, when suckling, to forage far and for long priods. By contrast, until the cubs are old enough to accompany first the male, and then both parents, the male stays in close proximity to the den and forages for short periods only.

During the present study bat-eared fox density in the study area was high, perhaps reflecting higher insect density resulting from 3 years of abnormally high rainfall. Increased prey density would result in the female being able to find enough food to sustain suckling entire litters, and also that the male could find enough food close to the den. Conversely, in drought years both the female and male may have trouble finding enough nourishment, in the case of the female to suckle the entire litter, and in the case of the male to be able to remain close enough to the den for effective defense of the young. Increased mortality in cubs could in such cases result from either lack of food (milk), or being taken by predators, which are common in the area, or a combination of both.

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COEXISTENCE IN TRANSVAAL CARNIVORA

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ABSTRACT

How coexisting carnivore species avoid interspecific competition is examined by consideration of their more prominent physical and behavioral characteristics. An attempt is made to explain coexistence of the 33 Transvaal carnivore species. The behavioral characteristics, which are considered here in various combinations, are daily activity regimen, food preference, habitat preference, geographical distribution, and social structure. The mean species body weight as an indicator of the size of prey on which a carnivore exists is also incorporated. Eighty-two % of the carnivores are shown to form a trend ranging from a nocturnal/solitary mode of life to an entirely diurnal/gregarious existence.

INTRODUCTION

Some two decades ago this paper might well have been titled "Niche occupation by Transvaal carnivores." The concept that each species fulfills a unique functional role in a specific place dates back to Grinnell (1924) and Elton (1927), and has served a useful function in subjectively describing the niche of an animal. However, it never really explained in detail how each animal fills its particular niche. Modern study of the niche and niche theory flows from Hutchinson's (1957) landmark paper, and allows quantification of the role each animal plays, from measurements of the amounts of various resources (axes in a hypervolume) utilized. Prior to this, Gause's (1934) experiments led to the idea that competition serves to separate species, and therefore the niches they fill. Competition through evolutionary time therefore led to separation of resource utilization in coexisting species, and the niches species occupy are therefore as much an outcome of evolution as, for example, their physical characteristics. On the other hand, although the physical characteristics of a particular species may be fairly constant over much of its distributional range, the exact niche it occupies (not in the descriptive Eltonian sense but in the analytical Hutchinsonian one) usually varies, depending on the habitat it occupies and the nature of other species in the community.

The mammal fauna of the Transvaal has been intensively surveyed over the last five years (Rautenbach, in preparation). This Province possesses a particularly rich mammal fauna, consisting of 175 species of which 33 are carnivores. Adaptation and radiation has led to different parts of resources being utilized, especially food and activity periods by different members of this assemblage of carnivores. It is of interest to note how resources are shared and competition lessened, and coexistence enhanced.

Rather than work out niche occupation by the various carnivores, which to be meaningful would involve quantifying resource utilization in various axes by carnivores in specific communities, the approach here taken is to look at various attributes of co-occurring species, and then to see where and if competition may come into force. This is done by considering in combination average species mass, basic food preference, daily activity regimen, habitat selection, distribution patterns, and specific social characteristics. Trends in adaptations are also considered, especially the advantage of differential body size in coexisting carnivores preying on the same food types, as variation in body size could affect prey size taken (Rosenzweig, 1966). It was also necessary to categorize behavior, in the full realization that the behavioral scope of each species may well be wider than the particular category to which it is designated.

Table 1.—*The 33 species of carnivores occurring in the Transvaal. Average body weight expressed in kg, the log. value of the mean body weight in grams, as well as the daily activity, social structure, and basic feeding categories to which each species is assigned, are indicated. See text for further explanations. I = Insectivorous, P = Predatory, O = Omnivorous, and S = Scavenging.*

Species	Average weight (kg)	N	Log. weight (g)	Daily activity regimen	Social structure	Basic feeding adaptation
Otocyon megalotis	3.4	(7)	3.53	iii	3	I
Lycaon pictus	22.0	(12)	4.34	v	5	P
Vulpes chama	2.9	(22)	3.46	i	1	P
Canis adustus	10.0	(5)	4.00	ii	1	O
Canis mesomelas	7.8	(48)	3.89	ii	2	O
Aonyx capensis	12.1	(4)	4.08	iii	3	I
Lutra maculicollis	4.5	(1)	3.65	ii	3	I
Mellivora capensis	8.9	(5)	3.95	ii	2	I
Poecilogale albinucha	0.4	(4)	2.60	ii	3	P
Ictonyx striatus	1.1	(10)	3.04	i	2	I
Viverra civetta	12.4	(5)	4.09	i	1	O
Genetta genetta	1.9	(15)	3.28	i	2	P
Genetta tigrina	1.9	(24)	3.28	i	2	P
Suricata suricatta	0.7	(19)	2.85	v	5	I
Paracynictus selousi	1.6	(39)	3.20	i	2	I
Cynictis penicillata	0.8	(20)	2.90	iv	3	I
Herpestes ichneumon	3.1	(14)	3.49	v	3	P
Herpestes sanguineus	0.5	(25)	2.70	v	1	P
Rhynchogale melleri	2.8	(1)	3.45	ii	1	O
Ichneumia albicauda	3.6	(1)	3.56	i	2	P
Atilax paludinosus	4.3	(5)	3.63	i	1	I
Mungos mungo	1.3	(7)	3.11	v	5	I
Helogale parvula	0.2	(13)	2.30	v	5	I
Proteles cristatus	9.9	(14)	4.00	i	1	I
Hyaena brunnea	36.1	(7)	4.56	ii	2	S
Crocuta crocuta	69.7	(8)	4.84	ii	4	P
Acinonyx jubatus	35.1	(3)	4.55	iv	2	P
Panthera pardus	41.7	(4)	4.62	ii	1	P
Panthera leo	204.1	(4)	5.31	ii	4	P
Felis nigripes	1.5	(8)	3.18	ii	1	P
Felis serval	9.6	(5)	3.98	i	1	P
Felis caracal	10.5	(10)	4.02	ii	1	P
Felis libyca	4.7	(58)	3.67	ii	1	P

METHODS

Table 1 lists the 33 carnivore species occurring within the Transvaal, with average weight, expressed in kg of both sexes combined, indicated for each species. Weight data are based on Transvaal Museum records, supplemented by relevant information from Smithers (1971). Samples sizes (N) are indicated. The logarithmic values for the means of species weights as expressed in g were calculated and are also given.

Based upon personal observations and unpublished data (Rautenbach, in preparation; Nel, in preparation), as well as published information (see Smithers, 1971; Rowe-Rowe, 1977*a*, 1977*b*), an integral numerical value has been assigned to the daily activity regime of each species. These range from exclusively nocturnal with a Roman numerical value of i, to exclusively diurnal with a numerical value of v (Table 1). Categories ii and iv denote nocturnal species with some diurnal activity, and diurnal species with occasional nocturnal activities, respectively. Similarly, integral Arabic numerical values 1 through 5 have been designated for the solitary to gregarious behavioral range, ranked from very solitary with a numerical value of 1, through to very gregarious with a numerical value of 5. The various species were each assigned to one of these five social category values on the grounds of average social grouping, allowing for other situations mentioned in the literature.

The integral values assigned to these two behavioral patterns considered (activity and social groupings) are only arbitrary points spaced along a continuum, and each represents an average categorized value considered most typical for the species. Judgment herein was subjective. We could not use more than five subdivisions with any accuracy, but in spite of this the resulting divisions are found to be both convenient and meaningful.

Hunting behavior is adapted to basic food preference. Diet and the mode of acquiring nourishment are other important aspects of the adaptive behavioral makeup of a species' accompanying avoidance of competition. Also considered in this study, then, are the four basic feeding methods or food types of carnivores, that is scavenging, omnivorous, insectivorous (denoting a diet of any invertebrate), and predacious. In assigning each species listed in Table 1 to a feeding category, it must be stressed that carnivores are opportunistic with regard to food items taken, especially under low interspecific competitive conditions. Only what is considered to be the primary or optimum feeding trait of a species when under more intense interspecific competition is considered here.

In Fig. 1 the integral values of the activity regimen and the social structure are plotted against each other for each species. Intraspecific social interrelationships are presented on the horizontal axis, and the activity regimen on the vertical axis. In Fig. 2 the four basic feeding categories are presented by vertical columns, each of which is divided into diurnal and nocturnal subsections. The nocturnal subsections are stippled. Each species was assigned to its appropriate column with regard to its basic feeding behavior and characteristic daily activity cycle. Position against the vertical axis was assigned by the logarithmic value of the average adult body mass, expressed in g. The principle is that clustering of species indicates possible interspecific competition, and vice versa. This is based on the correlation between the size of the predator and the size of the prey it can effectively handle, or usually catches. It has been calculated that the maximum mass of prey that can be handled with efficiency by an individual true predator is 1.5 times that of the predator itself. Group cooperation accounts for a higher ratio between the individual predator and the prey. It conversely follows that a big carnivore could not exclusively hunt very small prey because the energy gain herein would not warrant the investment in such an energy expenditure.

RESULTS AND DISCUSSION

Those species falling within the limits of behavioral values 1i, 1ii, 2i, and 2ii in Fig. 1, are all nocturnal and solitary, and represent the majority (58%) of the Transvaal Carnivora. The lines in Fig. 1 connect the upper values for both variables of this nocturnal/solitary block, with the upper values of the very gregarious and exclusively diurnal group (value 5v). All species falling between these two lines are considered to represent a trend from a solitary and a nocturnal existence to an entirely gregarious and diurnal mode of life. No less than 82% of all carnivores in the Transvaal follow this trend. *L. maculicollis*, *P. albinucha*, *O. megalotis*, and especially *A. capensis* are behaviorally intermediate between the two extremes within this trend. It is within this trend that interspecific competition is potentially the highest, as will be elaborated below. Three of the four species at the extreme diurnal/gregarious end of the trend (Fig. 1) are small insectivores and thus potentially in direct competition.

Eighteen % of the carnivore species under consideration do not conform to this trend, and have adopted a strategy, which seems to minimize possible competition. However, where four species have radiated toward a diurnal/solitary mode of life (*H. sanguineus* very successfully), only two species radiated a short distance toward a nocturnal/gregarious existence.

There are no extremely nocturnal/gregarious species (value 5i), although the lion and the spotted hyena are approaching this condition. A possible explanation for the poor radiation toward an extreme nocturnal/gregarious behavioral range could be the difficulty of maintaining group structure in the dark. Smaller gregarious species are mostly insectivorous and diurnal and finding food in the dark may also present difficulties, apart from the difficulty in locating predators in time. Schaller and Lowther (1969) consider the lion, in contrast to the wild dog, as incompletely adapted to a social life because lions frequently quarrel over the proceeds of a hunt. If their interpretation is correct, the true position of the lion on the graph in Fig. 1 may be more toward the left, and consequently even closer to the general trend.

C. crocuta is basically a nocturnal animal, but may also be active during the day. According to Kruuk (1966, 1972) the species tends to scavenge by day, and to become efficient pack hunters and killers by night. The spotted hyena has a complex matriarchal social system, with the females physically bigger than the males and dominating them. *C. crocuta* thus has radiated successfully some distance away from the trend, toward a nocturnal/gregarious existence.

Otocyon, although regarded by most as a nocturnal species, has a diurnal mode of life in undisturbed areas during winter. In settled areas, however, it becomes exclusively nocturnal. In discussing the eastward range extension of the species in the Transvaal, Pienaar (1970) mentions that it is exclusively nocturnal in the Kruger National Park, and ascribes this to a form of protective behavior of colonists in a new territory. In the Transvaal as a whole the species is almost entirely nocturnal, but on the other hand it occurs for the most part in this Province only in settled areas. Studies elsewhere (Nel, 1978) show that activity is perhaps correlated to the need to thermoregulate efficiently. Most observations on the bat-eared fox in the Transvaal are

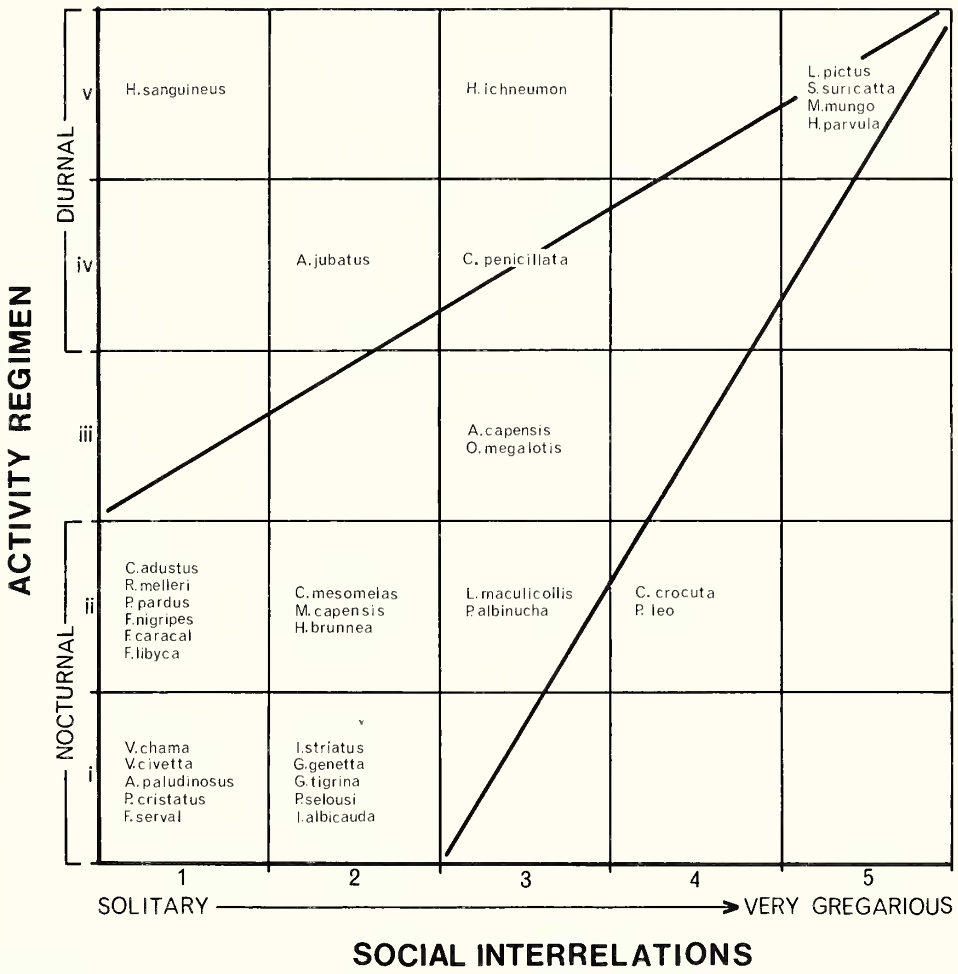

Fig. 1.—Graphical presentation of species separation by plotting the categoric values assigned to intraspecific social relations against the categoric values of daily activity cycles. See text for further explanations.

of solitary or small groups of animals, but again this would depend on the time of year of observations (Nel, 1978). This species is thus plotted in the position 3iii within the trend, although it could be argued that the Transvaal population should be plotted together with the lion just outside the trend.

It thus would appear that a vacuum exists at the nocturnal/gregarious end of the behavioral range, but that carnivores in the Transvaal do not utilize it, for reasons at present not fully understood.

H. sanguineus is the most predacious of the Herpestinae in the Transvaal, being an efficient killer of vertebrate prey. It is furthermore solitary and diurnal, in contrast to the general tendency for the more predatory small carnivores to be solitary and nocturnal (see Ewer, 1973:277). This seeming anomaly could result from an adaptive radiation to utilizing resources (especially habitat and food) with a low utilization pressure.

H. ichneumon and *C. penicillata* are only partly social species. When hunting for food both species are solitary and in this respect they are reminiscent of *H. sanguineus*. *H. ichneumon* is predatory, whereas *C. penicillata* is insectivorous. The distributional ranges of these two species furthermore do not overlap at all. *C. pencillata* is unique in the sense that when actively seeking food it is a solitary insectivore, in contrast to the other diurnal insectivores, which are social species.

The cheetah displays the three basic felid hunting techniques—stalking, utilization of the forepaws to fell its prey, and an oriented neck or choking throat bite according to the size of the prey. However, the cheetah atypically (for a felid) outruns its quarry

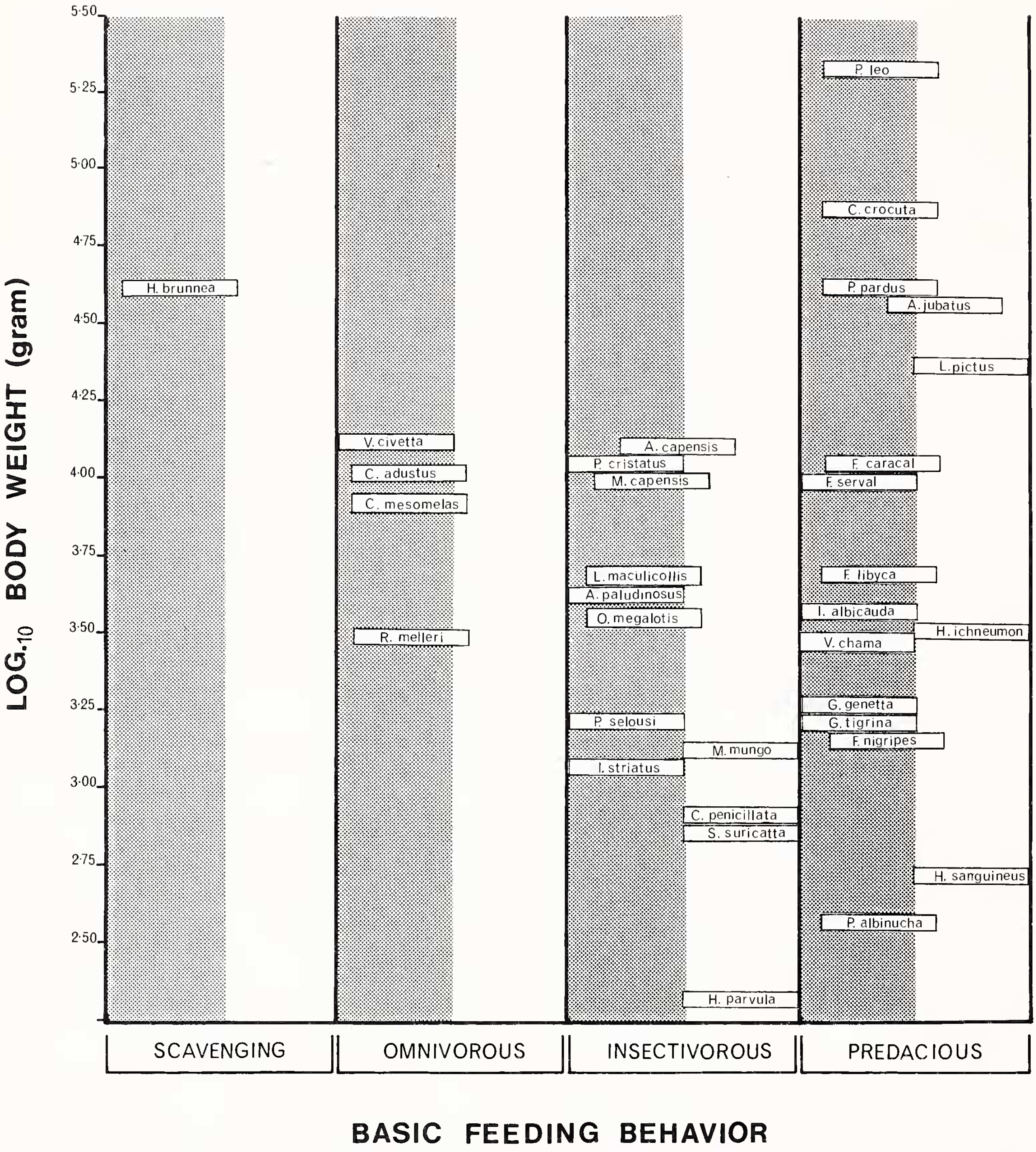

Fig. 2.—Graphical presentation of niche occupation. The four basic feeding categories are presented as vertical columns, each subdivided by a stippled column denoting nocturnal activity and an unstippled column denoting daylight activity. Species are assigned to their appropriate columns and are vertically spaced against the X-axis representing the log. value of the mean body weight in grams.

and possesses distinctive anatomical adaptations for this particular way of hunting, which can best be performed in daylight. There appears to be very little need for group participation. The cheetah thus clearly acquired behavioral and physical adaptations to enable it to radiate adaptively into a less competitive area. Of the four carnivores above the trend illustrated in Fig. 1, the cheetah utilizes a different trophic level as a result of its larger size. Yet the survival of the cheetah is threatened. Perhaps the reason for its precarious conservation status in the Transvaal should be sought in its low ranking position in the predator hierarchy. Cheetahs are often robbed of their prey by lions, leopards, and hyenas, and are even preyed upon by these more powerful predators (Schaller and Lowther, 1969; Pienaar, 1969).

A strong bias towards the insectivorous and predácious modes of life is evident (Fig. 2). The ratio of species between the four feeding classes is 1:4:12:16. Forty-eight % of Transvaal carnivores are predacious, which is considered to be the primary feeding trait of the Order. The remaining 52% have radiated away from a true predacious existence toward utilization of other protein resources, and have behaviorally adapted themselves to procuring them. Furthermore, no less than 75% of all species are predominantly nocturnal. The mean weight of the species in the omnivorous category is 8.25 kg, that of the insectivores is 4.07 kg, and the predators 25.82 kg.

We agree with Skinner (1976) that *H. brunnea* is basically a scavenger. This is further substantiated by the special dental and cranial adaptations acquired to cope with a scavenging way of life. Such a life style is for several reasons an uncertain existence, with chance playing no minor role. This is reflected in the single species represented in this category as well as the fact that it is primarily solitary, presumably in order to avoid excessive intraspecific competition for limited resources. Considering the apparent hardships of a scavenging life style, a lower mean weight may be an appropriate manner of reducing the energy requirements of the species. However, all indications are that the brown hyena is in all aspects primarily adapted towards capitalizing on the proceeds of the hunting endeavors of the larger predators.

An omnivorous life style is seen as the most opportunisitic of all, and can include as food items vertebrates (which are actively hunted), insects, carrion, and vegetable matter, especially fruit. The concept of a smaller body size as a means of reducing the energy requirements of the species with such a precarious existence can be illustrated by the fact that the mean species weight in the omnivorous category is only 8.3 kg, as opposed to the mean of 25.8 kg of the predatory category and mean of 36.1 kg of *H. brunnea* in the scavenging category.

R. melleri is much smaller than the other three species in the omnivorous category, and from this it is concluded that overlap in feeding interests is small. *V. civetta* is ecologically separated from *C. mesomelas* and *C. adustus*. The latter two species are inhabitants of the open plains and avoid forests. Like Smithers' (1971) findings, our own observations on *V. civetta* indicate a close association with riverine and subriverine woodlands. *C. adustus* is limited in range to the eastern Transvaal lowveld and a small area north of Pretoria. *C. mesomelas* ranges throughout the Transvaal. The two species are thus partly sympatric, and as is suggested in Fig. 1 may be in conflict here. Although Shortridge (1934) and Smithers (1971) speculate that *C. mesomelas* is being gradually replaced by *C. adustus* in the overlapping zone, this could not be demonstrated in the Transvaal. According to Pienaar (1963) *C. mesomelas* is numerically the more successful species in the Kruger National Park. *C. adustus* is however slightly larger than *C. mesomelas*, and indications are that it relies less on vegetable matter as a food source.

The insectivorous feeding category has the lowest mean body weight. This is considered as a significant adaptation to the small size of the individual prey, and the quantity and effort required on the part of the carnivore to fulfill its energy requirements. There are three clusters in this category that warrant closer scrutiny (see Fig. 1).

A. capensis is the biggest member of the insectivorous group. It is an aquatic mammal subsisting almost entirely on crabs (Rowe-Rowe, 1977*a*, 1977*b*). The terrestrial *P. cristatus* is the biggest carnivore living on Insecta, namely almost exclusively termites (especially *Triner vitermes*). It is not well equipped to dig out subterranean termites. *M. capensis* is also terrestrial and overlaps in range with the aardwolf. It however hunts invertebrates bigger than termites, especially spiders. The honeybadger is particularly well adapted to procuring this subterranean prey.

L. maculicollis, *A. paludinosis*, and *O. megalotis* also form a cluster in Fig. 1. The latter species is however a terrestrial inhabitant of the open plains, whereas the former two are to varying degrees semiaquatic. The spotted-necked otter and the marsh mongoose appear to be in conflict as they both rely heavily on crustaceans in their respective diets, and furthermore overlap in geographic range and habitat requirements. *A. paludinosus* is however a more versatile animal because it is more mobile on land. It wanders greater distances away from water and utilizes a wider spectrum of food resources. It is furthermore believed to hunt for aquatic prey only in the shallows, as opposed to *L. maculicollis*.

C. penicillata and *S. suricatta* also overlap in distributional range. Where the suricate is very gregarious and almost exclusively insectivorous, the yellow mongoose is a solitary hunter, which takes vertebrate prey as well as invertebrates.

The predatory category is the true domain of the Felidae, and no felid has radiated away from it. They are specialist killers, the only group capable of handling prey larger than themselves singlehanded. This is achieved mostly by means of a lethal well-directed single neckbite, or derivations thereof. Felidae are, in general, also expert stalkers.

Of the nonfelids in this feeding category, the mustelid *P. albinucha* is an exception, in that it behaves very similarly to the Felidae with regard to killing efficiency and the size of prey that it can handle. The remainder, that is the viverrids, canids, and *Crocuta*, all belong conditionally to the predatory category. *C. crocuta* and *L. pictus* rely on group cooperation to kill, and are relatively inefficient predators when alone. The remainder of the nonfelids rely on the other food sources already discussed, and when they kill, it is mostly prey much smaller than themselves (excluding domestic stock).

Very little is known of the serval, but from the information that is available, it would appear not to be in conflict with the caracal, as is indicated in Fig. 1. The serval appears to be restricted to areas with permanent surface water and its associated forests, and preys mostly on rodents. The caracal, on the other hand, does not prefer forests and is a true predator of prey more equal in size to itself.

The geographic ranges of *V. chama* and *I. albicauda* overlap only peripherally in the Transvaal. *F. libyca*, on the other hand, is widely distributed and overlaps with the ranges of both the former species. *F. libyca* and *V. chama* are separated in size to the extent that they presumably avoid conflict by means of differential choice in prey size. *I. albicauda* is restricted to riverine forests, whereas *F. libyca* has a wide habitat tolerance. The latter species therefore appears to be a universalist, the former a specialist extremely well adapted to its particular narrow niche. In the zone of contact between these two species, it can be postulated that *I. albicauda* has the edge in a competitive situation.

The two species of genets are partly sympatric. Our own experience agrees with that of Smithers (1971) in that these two species are ecologically separated. *G. tigrina* prefers a habitat close to water, whereas *G. genetta* exists away from it. The range of *F. nigripes* overlaps partially with that of *G. genetta*, and not at all with *G. tigrina*. However, so little is known about the general biology of the black-footed cat, that no suggestions can be offered as to how it avoids conflict with the small-spotted genet.

CONCLUSIONS

A behavioral trend is indicated in carnivores, which ranges from a direct correlation between a nocturnal/solitary mode of life, to an entirely diurnal/gregarious existence. We conclude that 82% of the Transvaal carnivores fall within this trend. Presumed adaptive radiation away from this trend is restricted to six species. Carnivores are considered incapable of adapting to an entirely nocturnal/gregarious life style.

In the majority of coexisting species interspecific competition is avoided, primarily through different food sources, differences in size of food items (correlated to different body size of the carnivores), or differential use of habitat types. However, in the instances of the two jackal species, *L. maculicollis* and *A. paludinosus*, as well as *F. nigripes* and *G. genetta*, at least partial interspecific competition is suspected. A more intimate knowledge of the general biology of these six species may in time show more subtle mechanisms of avoiding conflict.

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SYSTEMATICS OF THE HYRACOIDEA: TOWARD A CLARIFICATION

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ABSTRACT

Opinion is divided on whether the Order of the Hyracoidea contains three genera, *Procavia*, *Heterohyrax* and *Dendrohyrax*, or whether *Heterohyrax* should be regarded as a subgenus of *Dendrohyrax*. The anatomical and behavioral features here presented show that there is a roughly equal, definite distinction between all three, justifying a differentiation into three genera.

INTRODUCTION

The systematic relationships of the Hyracoidea are still open to many questions. The classification at the species level is not at all clear, and there are still divergent opinions about the number of genera in this Order.

Hahn (1935, 1959), in his revision of the Hyracoidea, distinguished three genera—the tree hyrax, *Dendrohyrax*, the bush hyrax, *Heterohyrax*, and the rock hyrax, *Procavia*. In more recent reviews, Bothma (1971) and Kingdon (1971) agree with Hahn, whereas Hayman (letter dated 29 October 1964 to C. R. S. Pitman, on file in British Museum [Natural History], London) and Roche (1972) maintain that there are only two genera, *Procavia* and *Dendrohydrax*, *Heterohyrax* being a subgenus of the latter. Roche even thinks it possible that *Dendrohyrax* and *Heterohyrax* may be merely different species; the only basis for his assumption is the small extent of cranial and especially dental distinction between these two. The molars are of brachydont structure in both, whereas *Procavia* has hypsodont dentition.

A new perspective may settle the controversy, and this paper therefore describes some anatomical features and behavioral aspects of *Procavia johnstoni matschiei* Neumann 1900, *Heterohyrax brucei dieseneri* Brauer 1917, and *Dendrohyrax arboreus stuhlmanni* (Matschie) 1892, as representatives for each genus.

METHODS

While studying the ecology and social behavior of the rock hyrax *P. johnstoni* and the bush hyrax *H. brucei* (Hoeck 1975, 1977 *a*, and in preparation) in the Serengeti National Park, Tanzania, in 1971–1973 and 1975–1976, over 350 animals were trapped, examined, and basic body measurements were taken before release.

Eight *D. arboreus*, living on fig trees (*Ficus natalensis*), in the Ngorongoro Crater floor were also trapped, measured, and observed for 10 nights.

Total body length and anus-preputial opening distance were measured with the animal lying stretched on its back. The anus-preputial opening measurement of one adult *Dendrohyrax validus* male from the West Kilimanjaro Forest was kindly supplied by Mr. P. Fox.

RESULTS

Anatomical Differences

Anus-preputial opening.—This measurement allows a clear distinction between males of the three species (Table 1). *H. brucei* males have twice the anus-preputial opening distance of *P. johnstoni* males, and over three times that of *D. arboreus* and *D. validus*.

Table 1 includes, for comparative purposes, the body weight and length of adult males (over 16 months). *H. brucei* and *D. arboreus* have identical measurements, whereas *P. johnstoni* is heavier and larger.

Penis structure.—There is a striking difference of penis structure in *D. arboreus*, *H. brucei*, and *P. johnstoni* (Fig. 1). *D. arboreus* males have a short, simply-built penis that is slightly curved. No evident difference was observed in the external penis anatomy of *D. arboreus* and *D. validus*. The penis of *H. brucei* is complex; on the penis end, and arising within a cup-like glans penis, is a short, thin

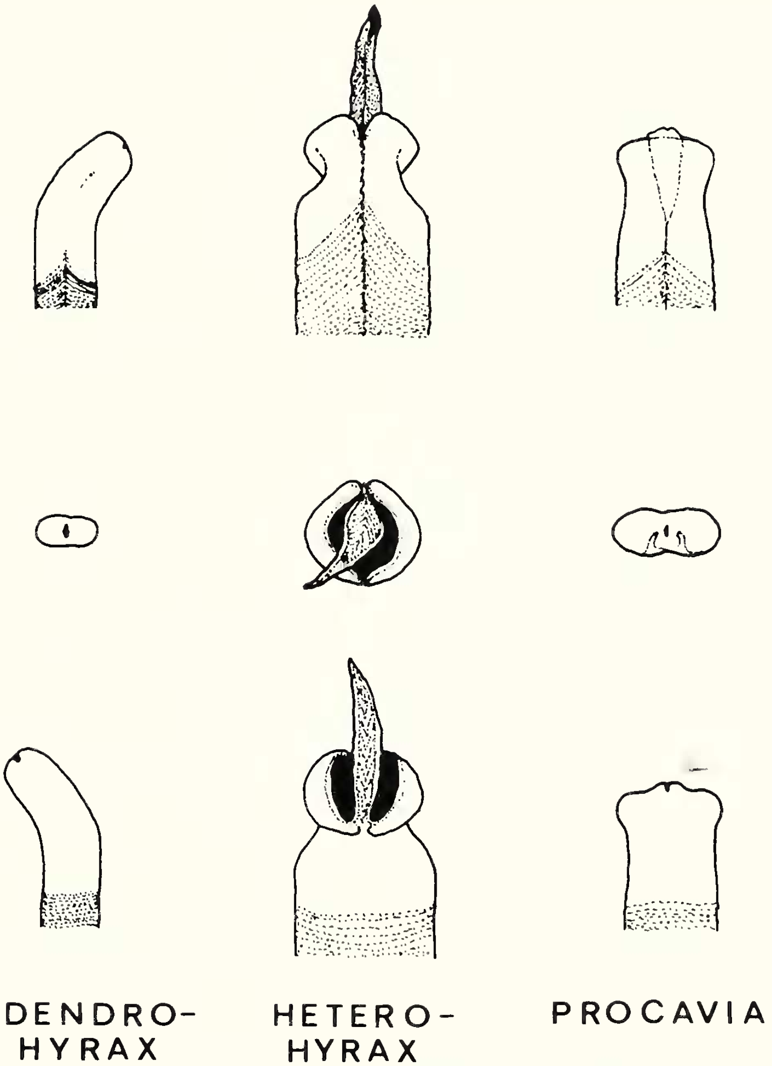

Fig. 1.—Diagram of external penis anatomy in adult males of *Dendrohyrax arboreus*, *D. validus*, *Heterohyrax brucei*, and *Procavia johnstoni*, showing approximate size relationship. Top, penis as viewed ventrally; middle, viewed from above the supine animal; bottom, dorsal view.

appendage, which has the penis opening. Fully erected, the little appendage also stiffens, the penis measures over 6 cm (Fig. 2). *P. johnstoni* have a short, simply-built penis with a slightly elliptical cross-section, the diameter increasing slightly toward the tip. More detailed features of the anatomy and histology of the penis of *Heterohyrax* and *Procavia* are given by Glover and Sale (1968).

Foot color.—The skin of the foot pads of *P. johnstoni* and *H. brucei* is black, whereas in *D. arboreus* it is pink. *D. arboreus ruwenzorii*, however, living among rocks in the Ruwenzori Mountains, Uganda, have black skin on these pads (T. Struhsacker, personal communication).

Behavioral Differences

Activity patterns and feeding behavior.—The long-term observations in the Serengeti showed that both *P. johnstoni* and *H. brucei* are diurnal. Although feeding times are identical, feeding behavior differs. *P. johnstoni* is mainly a grazer; *H. brucei* feeds almost exclusively on browse material. For further details see Hoeck (1975, 1976*a*, 1977*b*). The brief observations in the Ngorongoro Crater clearly established *D. arboreus* as nocturnal, browsing almost exclusively on *Ficus natalensis* and *Acacia albida* trees.

Mating behavior.—The following differences were observed in the mating behavior of *P. john-*

Fig. 2.—*Heterohyrax brucei* male and female just before copulation. Notice the length of the male's nearly-erected penis.

stoni and *H. brucei,* based on 14 and 21 observed copulations, respectively.

In *P. johnstoni,* usually after an initial mating call, the male executes weaving head movements, the penis is erected, and the dorsal hairs raised. The female presses her rump against the male's flank or breast. After mounting, the male grasps the sides of the female vigorously with his forelegs, makes several thrusting motions, the last being a short jerk, and then jumps down. Copulation lasts only a few seconds (Hoeck, 1976*b*).

In *H. brucei,* the male approaches the female, giving a short shrill call almost inaudible to humans, and both perform a short "dance" during which the male smells the vagina. He then mounts, holding the female's sides with his forelegs. With fully erected penis the male makes several thrusting motions, while swinging the head from side to side and sometimes opening his mouth, probably calling. The penis is not introduced, but pressed against the vagina. The position being maintained, the penis slackens; after 20 to 30 seconds several renewed thrusts are made with fully erected penis, but still without introduction. After some 3 to 5 min the penis is completely introduced with a sudden violent jerk, whereupon the female jumps, bites, and chases the male (Hoeck, 1977*c*).

Mating was not observed in *D. arboreus.*

The territorial call.—Adult males of *H. brucei, D. arboreus,* and *P. johnstoni* have very distinctive calls, as shown in the sonogram (Fig. 3).

The call of *H. brucei* is shrill and long, lasting about 1.5 seconds. It is given repeatedly for up to 5 min.

The calls of *D. arboreus* start with several cracking sounds, which are followed by a loud scream, repeated several times. The sonogram shows the transition between the cracking sounds and the scream. Several short cracking sounds follow immediately after each of the first few screams, whereas in the later part of the sequence the scream occurs alone.

The call of *P. johnstoni* is a repetitious bark, becoming longer and louder toward the end of the sequence, the last barks ending with gutteral noises. One of these last barks with the following gutteral can be seen in the sonogram.

Calls are loud in all three species (audible for several hundred meters, depending on wind conditions), and a calling sequence may last up to 5 min. In *H. brucei* and *D. arboreus* only the adult males were observed to produce these calls, whereas in *P. johnstoni* on rare occasions adult females made similar calls. The territorial calls became more frequent in *P. johnstoni* and *H. brucei* toward the mat-

Table 1.—*Anus-preputial opening distance, body weight, and total body length for adult males. Lengths were measured with the animals lying stretched on their backs.*

	Distance anus-preputial opening (cm)			Body weight (kg)			Body length (cm)		
Species	N	Mean	SD	N	Mean	SD	N	Mean	SD
Procavia johnstoni	41	3.5	0.91	66	2.95	0.72	43	48.68	4.47
Heterohyrax brucei	31	8.0	0.81	57	1.75	0.17	28	43.39	1.78
Dendrohyrax arboreus	2	1.7		2	1.62		2	43.85	
Dendrohyrax validus	1	2.5							

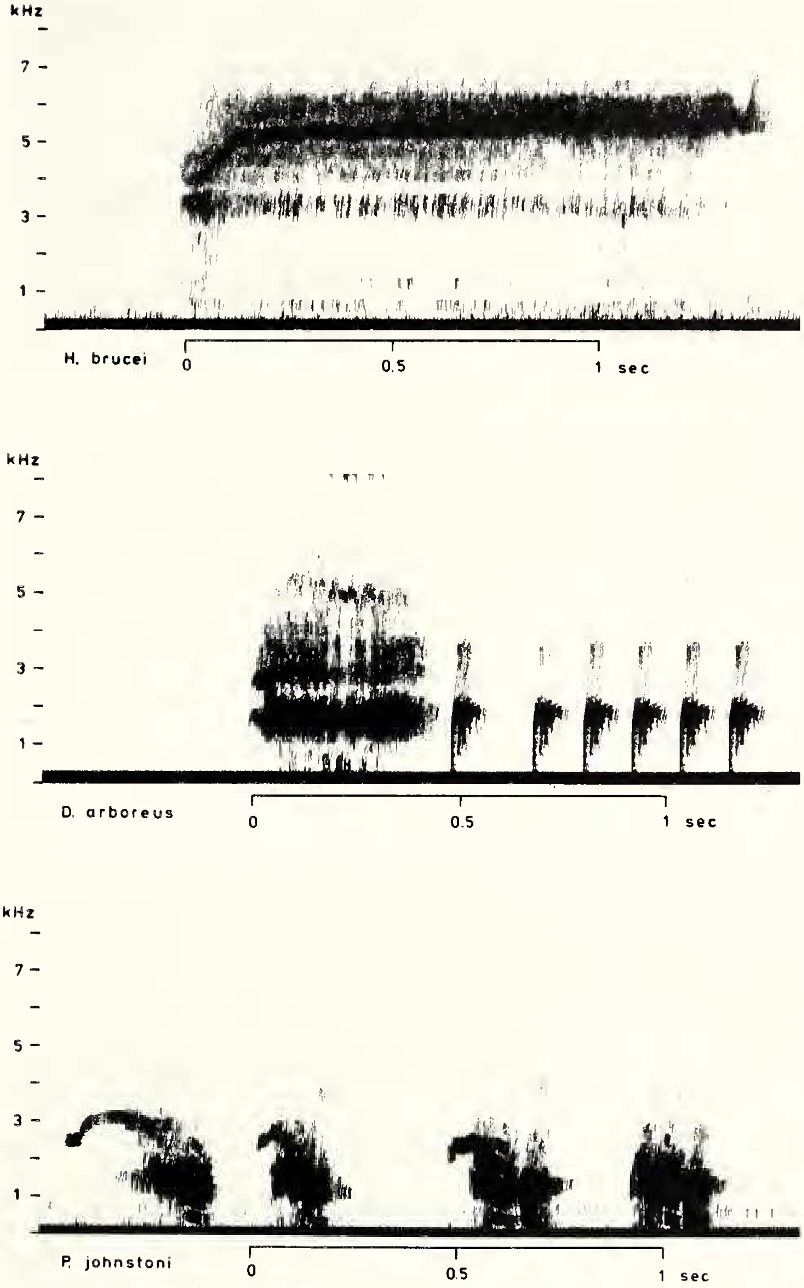

Fig. 3.—Sonograms of male territorial calls for *Heterohyrax brucei*, *Dendrohyrax arboreus*, and *Procavia johnstoni*. A calling sequence may last up to 5 min. Representative sounds from sequences are given for all three species.

ing season, and were usually made by territorial males (Hoeck, in preparation). The call of one territorial male may stimulate all others in the vicinity to call. Each animals's calls are so distinctive that they allow individual recognition by the human observer.

DISCUSSION

The anatomical and behavioral differences presented, namely penis anatomy, anus-preputial opening distance, and the territorial call, show *H. brucei* to be distinct from both *D. arboreus* and *P.*

johnstoni. As a browser, *H. brucei* resembles *D. arboreus,* whereas its activity pattern is identical with that of *P. johnstoni.*

Lönneberg (1916) and Hahn (1959) suggested that the variation in hyrax molar structure could be a dietetic adaptation; as grass is a relatively coarse material, grazers should be expected to have hypsodont dentition (high crowns with relatively short roots), whereas browsers, consuming softer food, should have brachydont dentition (short crowns with relatively long roots). Observation of the feeding behavior shows exactly this state of affairs. *P. johnstoni,* mainly a grazer, has hypsodont molars, whereas the browsers *H. brucei* and *D. arboreus* have brachydont dentition. If our studies are confined to a comparison of molar structure and feeding behavior, a very close relationship between *Heterohyrax* and *Dendrohyrax* seems to be established. But for a revision of the systematics of an animal group, as many taxonomic criteria as possible should be examined not only anatomical, but also genetical, ecological and behavioral parameters, to ensure accurate comparison and exact taxonomic grouping.

In a group of species the distribution of behavioral similarities and differences tend to be related with phylogenetic relationships within the group (Brown, 1975). Behavior is a preeminently suitable field for adaptation; it is regularly a pacemaker in evolution, that is, it precedes adaptive anatomical change (Mayr, 1958; Wickler, 1972). In selecting a behavior pattern for comparative analysis, it should ideally be highly stereotyped within a species, but variable across species. Such a species characteristic behavior pattern is, for example, the copulatory behavior as shown in the comparative study of muroid rodents by Dewsbury (1975).

The territorial call is so distinct in character that it can confidently be used as a simple method of locating and recognizing different species. By this means a population of *Dendrohyrax validus* was discovered and first reported for the Kenya coast (Seibt et al., 1977).

The distance between the anus and the preputial opening, first noted by Coetzee (1966), and the structure of the penis, are important and very useful features for a rapid taxonomic identification. The females reproductive tract has not so far been analyzed, but this may also show a characteristic structure.

These observations suggest that *Heterohyrax* is as far apart from *Dendrohyrax* as from *Procavia* and that one can differentiate three groups in the Hyracoidea no matter on which taxonomical level. Unless further studies, for example, genetic analyses, provide other evidence, I suggest that Hahn's (1935, 1959) and Bothma's (1966) recognition of three genera in the Order Hyracoidea should be retained.

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PATTERNS OF SPECIATION IN AFRICAN MAMMALS

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ABSTRACT

The distribution and speciation of African mammals can be interpreted in terms of both isolation and dispersal associated with Quaternary climatic and vegetational changes. Patterns of faunal diversity and endemism suggest the former existence of refugia in Forest Regions and dispersal between these Regions. Isolation has also been significant in savanna, but dispersal patterns are less easily assessed here. In certain superspecies, the directions involved in dispersals can be ascertained from the distribution of primitive and derivative character states, which in turn imply the cotemporal existence of ancestral and descendant taxa. Long term "ecological translation" in speciation appears to have occurred down the faunal diversity gradient, especially across the forest-savanna boundary, but also from savanna to arid zones. Different mammalian taxa have speciated in different ways and there are other impediments to the reconstruction of speciation patterns.

INTRODUCTION

Currently much attention is focusing on the historical geography and speciation of tropical biota. This paper, based on the literature and on my own taxonomic and faunistic studies mostly still in progress, draws attention to some of the main problems involved in assessing the speciation of African mammals during the fluctuating climatic conditions of the Quaternary.

The study of mammalian speciation seeks to describe the dispersion and geographic variation of species accurately, to identify hybrid zones and other types of apparent secondary contact, and to recognize primitive and derivative characters in the species being studied. It then attempts to infer localities of refugia occupied under adverse climatic conditions and to identify directions taken during periods of dispersal. It may be possible to provide a relative chronology of events (Table 7); hypotheses of this kind gain conviction if several mammals appear to have had similar histories. Finally, it may be possible to provide more absolute chronologies, with the assistance of other disciplines, and to trace the histories of regional faunas. Many difficulties are involved in this exercise.

TERMINOLOGY

Superspecies are "monophyletic groups of entirely or essentially allopatric species too different to be included in a single species" (Mayr, 1963:44). In the plural, the term is used (Bigalke, 1972) to embrace "monospecific" superspecies as well. Allospecies are species which are members of superspecies. Semispecies are either highly distinctive subspecies or full species whose status is debatable. Species groups are monophyletic assemblages of closely allied or sibling species, some of which may be allopatric, so that the term superspecies is inappropriate (Hall and Moreau, 1970). Subspecies groups are monophyletic groups of subspecies, which may approach species status.

SPECIATION AND ZOOGEOGRAPHY

Previous Studies

Interest in the evolutionary geography of African mammals dates from the early part of this century, with the publication of general interpretations of present faunal distributions in terms of Tertiary and Quaternary phenomena (Schwarz, 1924, 1926*a;* Lonnberg, 1929; Braestrup, 1935) and evolutionary studies on particular taxa, including the African buffalo, *Syncerus caffer* (Christy, 1924*a*, 1924*b*, 1929; Malbrant, 1935), monkeys, *Cercopithecus* and *Colobus* (Schwarz, 1926*b*, 1928, 1929), sunsquirrels, *Heliosciurus* (Ingoldby, 1927) and hartebeest, *Alcelaphus* (Ruxton and Schwarz, 1929). Two of these papers (Schwarz, 1928; Ruxton and Schwarz, 1929) were presented as the first parts of a series on the speciation of African mammals, but there was no sequel and after such a promising beginning, no progress in the subject was made for 20 years. The works mentioned had so little impact that only Lonnberg's and Braestrup's gained passing mention by Moreau (1952), and none is discussed by Moreau (1963, 1966) or Hamilton (1976).

Nevertheless, Lonnberg (1929) had already proposed that Pleistocene climatic cycles, by breaking up and uniting habitat types, were important in initiating the speciation of African mammals.

It was not until after the Second World War that a gradual reawakening of interest in mammalian historical biogeography developed. Booth contributed studies on evolutionary geography of West African mammals (Booth 1954, 1958*a*, 1958*b*) and a reappraisal of Schwarz's (1928) work on speciation in the mona monkeys. Blancou (1954) and Grubb (1971) reassessed Christy's (1929) and Malbrant's (1935) contributions on speciation in the African buffalo. Brain and Meester (1964) analyzed speciation in southern African *Myosorex*, Groves (1971) the evolutionary dispersal of the gorilla, and Dieterlen (1971) speciation of *Dendromus*. Jotterand (1972), following the work of Matthey, discussed chromosome evolution in relation to the speciation of *Mus*. Eisentraut (1973) investigated the Pleistocene history of Fernando Po and the Cameroon highlands. Most recently, Kingdon (1971, 1974*a*, 1974*b*) has presented hypotheses to account for patterns of speciation in many African mammalian taxa.

Much important taxonomic and faunistic work continues to appear, of course, but the opportunity for adopting an evolutionary outlook does not always arise.

Speciation and Quaternary Climatic Changes

The concept that animal distribution and speciation in Africa have been strongly influenced by cycles of arid and moist climatic phases has become well established, with the work of Moreau (1952, 1963, 1966), Carcasson (1964), and other non-mammalogists. Hamilton (1976) has reviewed the evidence for climatic change implicit in the present geography of forest biota, whereas Livingstone (1975) has covered the geological and palynological evidence; the phenomenon of climatic change is well documented for Quaternary Africa, though only the more recent events can be reliably dated. We have emerged from a relatively short moist phase, dating back 10,000–12,000 years BP; prior to this there was a longer dry episode commencing at least 22,000 years BP. The periodicity of earlier paleoclimatic episodes is still uncertain, but cycles of moist and arid phases are presumed to have succeeded each other throughout the Pleistocene. These cycles led to contraction and expansion, disruption and fusion of the major vegetation zones. Mammal populations associated with a particular vegetation type were thus restrained from dispersing at one period and perhaps even restricted to small refugia, yet were free to disperse at other times and invade adjacent expanding ex-refugia coalescing with their own.

Table 1.—*Incidence of allospecies and superspecies in mammalian taxa in Africa.*

Taxa	No. of species	No. of superspecies	No. and proportion of species which are allospecies	Species/superspecies ratio
Carnivores	70–76	59	24–33 (0.34–0.43)	1.2–1.3
Artiodactyls	85–96	64	36–52 (0.42–0.54)	1.3–1.5
All ungulates	95–112	72	39–63 (0.41–0.56)	1.4–1.7
Primates	45–69	30	25–49 (0.56–0.71)	1.5–2.3
Squirrels	37	26	17 (0.46)	1.3

Ideally, the most complete form of speciation is for one species to evolve into two sympatric species. Climatic change in Africa and the response of mammal populations facilitated the isolation and dispersion necessary for this to occur. During the isolation phase, regional differentiation was emphasized and potential mechanisms of reproductive isolation developed, whereas in the expansive phase, sympatry with former conspecifics was acquired. However, the expansive phases also provided the potential for producing further isolates, through the extension of distribution into what would become refugia once again in the next phase of the climatic cycle. Expansive phases were longest for eurytopic species, which may have continued to disperse without check, but shortest for stenotopic species differentiating in isolation. Expansive and isolating phases may have been antitemporal in forest and nonforest species, moist phases producing continuous forest, disrupting savanna, and dry phases the reverse (maps in Carcasson 1964 and Hamilton 1976).

It is difficult to believe that selection remained uniform during these cycles and it is tempting to speculate that the expansive phase was a time of more rapid phenetic change in populations at the dispersive front, which were increasing in numbers, encountering new habitats and establishing an ecological niche that had been locally unoccupied. In other words, it may be possible to regard the expansive phase, rather than the geographic disruption of populations, as the initiating element in speciation—that speciation occurs not so much by the

Table 2.—*Secondary contact between species and well-differentiated subspecies.*

1. Secondary intergradation: hybrids or intermediates known
   - (a) *Rhychocyon cirnei, R. petersi,* Tanzania (Kingdon, 1974*a*, but not Corbet and Hanks, 1968)
   - (b) *Paraxerus cepapi, P. palliatus,* Tanzania (Kingdon, 1974*b*)
   - (c) *Cercopithecus (aethiops) tantalus, C. (a.) pygerythrus,* Uganda (Dandelot, 1959)
   - (d) *Cercopithecus (mitis) mitis, C. (m.) Albogularis,* (Booth, 1968)
   - (e) *Cercopithecus erythrotis, C. cephus,* Cameroon (Struhsaker, 1970)
   - (f) *Papio anubis, P. cynocephalus,* Kenya (Maples, 1972)
   - (g) *Papio cynocephalus, P. ursinus,* Zambia and Malawi (Freedman, 1963)
   - (h) *Papio anubis, P. hamadryas,* Ethiopia (Gabow, 1975, and references therein)
   - (i) *Genetta tigrina, G. rubiginosa* (that is, *pardina*?), Natal (Pringle, 1977)
   - (j) *Dendrohyrax dorsalis, D. arboreus,* Uganda (Kingdon, 1971)
   - (k) *Giraffa camelopardalis reticulata, G. c. tippleskirchi,* Kenya (Stott, 1959)
   - (l) *Kobus (ellipsiprymnus) defassa, K. (e.) ellipsiprymnus,* Kenya (Backhaus, 1958)
   - (m) *Alcelaphus (buselaphus) lelwel, A. (b.) tora* subsp., *cokei* in Kenya, *tora,* along Sudan-Ethiopian border (Ruxton and Schwarz, 1929)
   - (n) *A. (b.) major, A. (b.) lelwel,* Central African Empire (Malbrant, 1952)
   - (o) *Syncerus (caffer) nanus, S. (c.) caffer,* Zaire (Grubb, 1971)
   - (p) *Loxodonta (africana) cyclotis, L. (a.) africana,* Uganda (Bere, 1962; Laws et al., 1975)

2. Allospecies or semispecies potentially in contact, but no hybrids, intermediates or localized sympatry known
   - *Funisciurus pyrrhopus, F. substriatus,* Ghana
   - *Paraxerus vexillarius, P. byatti,* Tanzania
   - *Paraxerus ochraceus, P. cepapi,* Tanzania
   - *Heliosciurus gambianus, H. mutabilis,* Tanzania
   - *Xerus inauris, X. princeps,* South West Africa
   - *Manis gigantea, M. temmincki,* Zaire, Central African Empire?
   - *Arctocebus calabarensis, A. aureus,* Cameroon
   - *Galago senegalensis, G. inustus,* Zaire
   - *Cercopithecus cephus, C. ascanius,* Congo
   - *Cercopithecus erythrogaster, C. erythrotis,* Nigeria
   - *Cercopithecus pogonias, C. denti,* Zaire
   - *Cercocebus torquatus, C. agilis,* Rio Muni and Gabon
   - *Papio papio, P. anubis,* Guinea
   - *Mandrillus sphinx, M. leucophaeus,* Cameroon
   - *Potamochoerus (porcus) porcus, P. (p.) larvatus,* Zaire
   - *Cephalophus ogilbyi, C. callipygus,* Cameroon; Gabon
   - *Cephalophus nigrifrons, C. natalensis,* Kenya
   - *Cephalophus nigrifrons, C. rufilatus,* Zaire
   - *Madoqua saltiana, M. piacentinii,* Somalia
   - *Gazella soemerringi, G. granti,* Ethiopia
   - *Gazella dorcas, G. spekii,* Somalia
   - *Alcelaphus lichtensteini, A. buselaphus,* Tanzania
   - *Tragelaphus (scriptus) scriptus* and *T. (s.) sylvaticus,* Sudan

Table 2.—*Continued.*

3. Marginal sympatry
   - (a) *Elephantulus rufescens, E. revoili,* Somalia (Corbet and Hanks, 1968)
   - (b) *Elephantulus brachyrhynchus, E. fuscus,* Mozambique (Corbet 1974)
   - (c) *Cercopithecus nictitans* and *C. mitis,* Zaire (Schouteden, 1944–1946)
   - (d) *Cercopithecus mona* and *C. pogonias,* Cameroon (Schwarz, 1928; Struhsaker, 1970, records hybrids)
   - (e) *Cercopithecus mona* and *C. campbelli,* Ghana (Booth, 1955)
   - (f) *Colobus guereza* and *C. angolensis,* Zaire (Schwarz, 1929; Schouteden, 1944–1946)
   - (g) *Colobus guereza* and *C. satanas,* Cameroun (Schwarz, 1929)
   - (h) *Helogale hirtula, H. parvula,* Somalia (Azzaroli and Simonetta, 1966)
   - (i) *Herpestes ochraceus, H. sanguineus,* Somalia (Azzaroli and Simonetta, 1966)
   - (j) *Genetta angolensis, G.(genetta) felina,* Angola (Cabral, 1969)
   - (k) *Madoqua guentheri, M. kirkii,* Kenya (Hollister, 1924)
   - (l) *Redunca redunca, R. arundinum,* Tanzania (Vesey-Fitzgerald, 1964)
   - (m) *Gerbillurus vallinus* species-group, South West Africa (Schlitter, 1973)
   - (n) *Aethomys namaquensis, A. granti,* South Africa (Davis, 1974)
   - (o) *Mus mahomet, M. proconodon,* Ethiopa (Yalden et al., 1976)

break up of a continuous distribution, else there would be a tendency for distributions to get smaller and smaller, but by dispersal and then isolation of ancestor and "dispersate." Chains of primitive-derivative allospecies (Table 6) can be interpreted through this hypothesis. More stable populations, away from the dispersal front, may have been more subject to a stabilizing selection.

The model discussed so far may apply to the speciation of certain mammals, yet it is not easy to arrange case histories in a sequence representing earlier and later stages of the process, because of "taxon effects" and because of the inadequacy of our data.

Speciation Patterns in Different Mammalian Taxa

The mammalian orders in Africa differ in species dispersion and interspecific relations, suggesting different modal forms of speciation.

African carnivores are ecologically tolerant and broadly distributed; only seven of 21 forest species are confined to a single Forest Region, only eight of 25 savanna species to a single Savanna Zone.

Thirteen species extend outside the continent, another five are essentially non-African, and six occur widely in both forest and savanna. There are relatively few allospecies (Table 1), although six species can be regarded as very highly differentiated vicariants of tropical Asiatic carnivores. Ungulates are not so widespread. Fifteen of 31 forest species are found in a single Forest Region, 24 of 39 savanna species are restricted to a single savanna zone. Six are essentially non-African; no chiefly African species extends outside the continent. Ungulates show a greater tendency to form superspecies and, in addition to the figures given (Table 1), there are another 16 to 20 species showing very strong geographic variation, which are hence incipient superspecies (there are only one or two cases like this in the carnivores). Except for *Papio hamadryas* in Arabia, no primate or squirrel ranges outside Africa. Primates are even more restricted in distribution; even with a conservative classification, 20 of 34 forest species are found in a single Forest Region. They also show a still stronger tendency to form superspecies. This is not merely because they are predominantly forest animals, more subjected to isolation and differentiation, for even among forest mammals they show an unusual tendency to break up into discrete taxa, to form montane subspecies, and to show complex patterns of dispersive semispeciation (Table 8). Although squirrels have the same superspecies to species ratio as carnivores, very few species are widely distributed—23 of 29 forest species are confined to single Forest Regions—and some speciation has been rather localized, evidently without repeated dispersions throughout the forest biome. There are at least four sibling species-pairs in *Funisciurus* and *Paraxerus*, so that sympatric species are more alike and more closely allied than some allospecies; the *cepapi-palliatus* group of *Paraxerus* probably constitutes a "ring species." Species in many genera of other small mammals also form superspecies (for example, the *Tatera afra* group, Davis, 1966). Bigalke (1972) indeed has classified all African mammals into superspecies and his figures give 1.4, 1.1, and 1.4 species per superspecies for shrews, bats, and rodents, respectively. However, in these groups generally, even more than in the particular case of squirrels, there is such frequent sympatry between similar or sibling species (for example, *Lemniscomys striatus* and *L. macculus*) that the superspecies concept is inadequate on its own. Many genera can reasonably be classified into "species groups," (Hall and Moreau, 1970) when a superspecies classification is not appropriate. Species of the genus *Arvicanthis* provide a good example.

Contact between species thus ranges from allopatric to sympatric and involves varying degrees of genetic introgression. With African mammals, however, very few cases of hybrid zones and related phenomena of secondary contact have been adequately described, and many are known only from brief notes or locality records on museum specimen labels. Less than 20 examples of secondary contact between semispecies and allospecies of the "larger" mammals are on record (Table 2); most are among the primates and artiodactyls, the taxa most prone to form superspecies, and the majority are in eastern Africa, along or to the east of the Western Rift. Examples f,h,i,l,m and o involve narrow hybrid zones; b,c and k concern broad zones of genetic introgression; in d,e and j, only a few hybrids are on record, and the other cases are not clear. There are at least 20 additional species-pairs, which are parapatric yet not separated by a major river barrier, where neither intermediate specimens nor localized co-occurrence are (yet) known. In a number of examples, notably monkeys along the lower Congo (Schouteden, 1944), allospecies are separated by major rivers, and in even more cases, semispecies do not even come close enough to make contact. Thus, although there are indications that contact between essentially allopatric populations involves a range from a considerable amount of gene exchange to none at all, the vast majority of relationships between allospecies and semispecies of the larger mammals—and there are more than 100 such relationships—requires evaluation in order to assess where they lie within this range. The formal taxonomy of these mammals implies a level of biological knowledge that has simply not been attained.

Among the "smaller" mammals, no hybrid zones have yet been discovered in Africa; a few cases of rather narrow sympatry between nearest-allied species are known (Table 2). The relatively large number of genera apparently with sympatric siblings includes *Crocidura*, *Epomophorus*, *Nycteris*, *Rhinolophus*, *Pipistrellus*, *Eptesicus*, *Glauconycteris*, *Scotophilus*, *Miniopterus*, *Tadarida*, *Funisciurus*, *Paraxerus*, *Graphiurus*, *Tatera*, *Dendromus*, *Malacomys*, *Aethomys*, *Lemniscomys*, *Arvicanthis*, *Praomys*, and *Mus*.

In summary, the following taxonomic differences in speciation appear to exist. Carnivores are broad-

Fig. 1.—Faunistic divisions of the Forest Biome in Africa, with presumed major Refugia (of more extreme arid phases) stippled; minor and more recent Refugia of less extreme arid phases probably occurred in intervening zones. W = Western Region, bounded by Dahomey Gap; WC = West Central Region, bounded by Oubangui-Congo Rivers, S = Sanaga River, O = Ogoue River, marking off subdivisions of the Region; EC = East Central Region, bounded by Congo River; SC = South Central Region; E = Eastern Region, boundaries only indicated, the forest itself restricted to many small riverain, mountain, and coastal "forest islands."

ly distributed so they rarely have the opportunity to form isolates and allospecies, hence they speciate less frequently. Primates and ungulates commence speciation more frequently but are not equally able to complete its later stages so as to acquire sympatry. When they do, it is only after repeated phases of isolation and dispersion, hence the existence of hybrid zones involving different levels of genetic isolation. These mammals could also evolve within the superspecies by elimination and replacement of allospecies without new sympatry being acquired (see Martin, 1972). Rodents and other small mammals speciate fast, and isolates readily become sympatric. Few chains of allopatric allospecies develop and a single sequence of isolation and dispersal can lead to speciation. Sibling sympatric species are not uncommon, but hybrid zones may be few. Evolution of chromosomes has been conspicuously important in developing mechanisms of reproductive isolation (see, for example, Jotterand, 1972).

Isolation in the Speciation of Forest Mammals

Based on geographical variation in its fauna, the lowland forest zone of Africa can be divided into a number of Regions (Misonne, 1963:87–88; Rahm, 1965, 1966, 1972), parts of some having presumptively been refuges for their fauna in past arid periods (Booth, 1958*a:* 59; Kingdon, 1971:65). Today these refuge areas are both foci of higher precipitation and centers where the regional fauna is rich-

Table 3.—*Numbers of superspecies including semispecies of "larger" mammals in presumed Refuges of major Forest Regions, and in minor Regions.*

Refuges and regions	Total superspecies	Endemic superspecies	Total species	Endemic species
Western Refuge	58	7	58	23
West-Central Refuge	68	10	69	17
East-Central Refuge	71	12	71	16
South-Central Region	51	4	51	11
Eastern Region	29	4	34	23

Table 4.—*Numbers of species of "larger" mammals in Forest Regions and numbers shared with other Regions.*

Forest Regions	Western	West-Central	East-Central	South-Central	Eastern
Western	58	44	33	26	8
West-Central	44	69	50	27	9
East-Central	33	50	71	39	10
South-Central	26	27	39	51	10
Eastern	8	9	10	10	34

est. The terminology of Regions and Refuges has not been standardized and is cumbersome, so I propose a simplified set of names (Fig. 1).

In discussing the numerical strength of the regional fauna (Tables 3, 4), the shrews, bats, and muroid rodents are omitted, as their species limits and distribution are less completely known. The remaining "larger" mammals of the forest constitute 165 species and semispecies in 103 superspecies. Only eight superspecies occur wholly outside the former major refugia (Western, West-Central, and East-Central)—*Allenopithecus nigroviridis*, *Cephalophus adersi,* and six squirrels, for which the term superspecies when applicable implies a younger evolutionary unit than in other orders. The number of species occurring outside the major refugia is 39 (24% of total), or 49 (30%) if isolates from the Mt. Cameroon and Ogooué subregions are considered. This distribution pattern of superspecies and species is not inconsistent with Booth's (1958*a*) view that a severe Quaternary arid phase restricted the distribution of the forest fauna almost entirely to the major refugia and that a subsequent moist phase led to its dispersal and then the differentiation of derivative subspecies, semispecies and, at least in squirrels, species, outside the principal refugia as a consequence of a later and less severe arid period (*ca.* 22,000 years BP ?). This derivative component of the forest fauna is distributed principally in the South-Central and Eastern Forest Regions.

The forest faunas decline in diversity towards the periphery of the Regions (Booth, 1958*a*, for the Western and West-Central faunas; Misonne, 1963, and Kingdon, 1971, for the East-Central and Eastern fauna). Endemics of different Regions overlap in distribution as well, but the overlap zones lie outside the principal refugia (Booth, 1958*a*, for the Western and West-Central faunas; Kingdon, 1971, for the East-Central and Eastern faunas, of his "northern" and "southern" forests and dispersal routes). It has been customary to make faunal zones strictly allopatric, but evidently they can also be treated cartographically as overlapping entities.

Each Forest Region shares more species with the nearest and fewer with more distant Regions (Table 4), except for the major discontinuity between the East-Central and Eastern Regions. The Western Region has a relatively high level of endemism (40%, Table 3) compared with any of the Central Regions, though collectively their level of endemism is similar (38%). Presumably this reflects the greater continuity of the Central Regions and the separation of the two major forest blocks by the Volta-Niger interfluvial area, and within it the Dahomey Gap (Booth, 1958*a*).

The presence of strongly marked endemic subspecies, allospecies, and full species north of the Sanaga around Mt. Cameroon, and again around the Ogooué valley to the south (Table 5), both areas lying outside the Refuge itself and having a depleted complement of the West-Central fauna, suggests a relatively complex history for this major Region. In a few instances, taxa in these separated subregions have a special affinity with each other. Thus, the monkey *Cercopithecus cephus* is replaced north of the Sanaga by *C. erythrotis,* yet populations of *C. cephus* transitional towards *C. erythrotis* (*C.c. cephodes*) occur far to the south, around the Ogooué delta. Some of the unique elements in the Mt. Cameroon area reflect probable faunal traffic with the East-Central and Western Regions, avoiding most of the West-Central Region itself; others may have diverged in subsidiary refuges adjacent to the West-Central Refuge.

The relatively impoverished (Misonne, 1963) South-Central Region shares more species with the East rather than the West-Central zones, the lower Congo acting as a barrier. It also has few endemic superspecies, implying a derivative origin of its fau-

Table 5.—*Vicariants, endemics, and localized species in the West-Central Forest Region.*

Genera	North of Sanaga	Sanaga to Ogooué	Ogooué Basin and South
Galago	*e. pallidus*	*e. elegantulus*	*e. elegantulus*
Arctocebus	*calabarensis*	*aureus*	—
Cercopithecus	*erythrotis*	*c. cephus*	*c. cephodes*
Cercopithecus	*mona* and *p. pogonias*	*p. grayi*	*p. nigripes*
Cercopithecus	*n. martini*	*n. nictitans*	*n. nictitans*
Cercopithecus	*preussi*	—	—
Miopithecus	—	*talapoin*	*talapoin*
Mandrillus	*leucophaeus*	*sphinx*	—
Colobus	*badius preussi*	—	—
Colobus	—	*satanas*	—
Heliosciurus	*rufobrachium*	*rufobrachium*	*gambianus*
Epixerus	—	*wilsoni*	*wilsoni*
Paraxerus	*cooperi*	—	—
Funisciurus	*isabella* only	*isabella* and *lemniscatus*	*lemniscatus* only
Funisciurus	—	—	*duchaillui*
Funisciurus	*p. raptorum*	*p. pyrrhopus*	*p. pyrrhopus*
Genetta	*cristata*	*servalina*	*servalina*
Hylochoerus	—	*meinertzhageni*	—
Cephalophus	—	*leucogaster*	*leucogaster*
Cephalophus	—	*nigrifrons*	*nigrifrons*
Cephalophus	*o. ogilbyi*	*callipygus*	*o. crusalbum*
Neotragus	*batesi*	*batesi*	—
Tragelaphus	—	*eurycerus*	*eurycerus*

na. There are a few species in the forests of northwest Angola not found in the Cuvette Central, which appear to have crossed the lower Congo rapids (*Funisciurus pyrrhopus, Lophuromys sikapusi, Anomalurus beecrofti, Miopithecus talapoin, Crossarchus ansorgei,* perhaps *Protoxerus stangeri loandae*), whereas *Funisciurus congicus* appears to have had a similar dispersal but has extended eastward as well, perhaps giving rise to the sibling *F. interior.*

The Eastern Forest Region corresponds to Kingdon's (1971) Southern Forest with its fauna dispersed along a "southern" route. It is actually an archipelago of montane and lowland, mainly coastal, forest. No single refugium could have existed in the Region during arid periods and there have been many opportunities for isolation and speciation. At least four superspecies are represented by two or more allospecies and several allospecies are very localized. Of the Region's 29 superspecies, 20 are found in every one of the other Forest Regions and only four are endemic. Though so poorly represented at this level, the Western Region's proportion of endemic species and semispecies is quite exceptionally high (65% of total), even though its species diversity is rather low. Hence we may presume that only widely dispersing superspecies have been able to reach this area, and relatively recently too, and that the area is a faunal sink.

A few essentially forest mammals such as *Colobus guereza* are distributed outside the major refugia or the other regions discussed so far, and must have diverged, initially at least, in forest galleries.

Dispersal in the Forest Biome

Some indication of dispersal routes within the forest can be obtained from distribution patterns. For instance, species with highly discontinuous distributions, such as *Anomalurus pusillus,* could have dispersed through areas presently occupied by more eurytopic forest species with more continuous distributions (for example, *Heliosciurus rufobrachium*) when gradients in forest type (Hall and Swaine, 1976) were differently distributed during pluvials (Livingstone, 1975), providing a more continuous suitable environment. Other dispersal trends between the forest zones are implicit in the degree of affinity of their faunas. But certain distributions suggest there has been dispersal between the Western and East-Central Regions, avoiding the West-Central Refuge but involving Mt. Cameroon and probably following a path north of the present northern limits of the forest. The presence of *Rhinolophus maclaudi* and *Micropotamogale lamottei* in the Western Refuge and of *R. ruwenzorii* and *M. ruwenzorii* in the highlands of the East-Central Refuge suggests one such ancient faunal continuity. More recent may be the dispersal, which accounts for the discontinuous distribution of certain montane mammals of the Cameroon and East-Central highlands. Groves (1971:49) has hypothesized that from a montane origin in the Albertine Rift highlands, the gorilla dispersed from east to west, Schaller (1963:29) believed that this dispersal was along a route north of the Uele River. Mona monkeys, mangabeys, red colobus, black and white colobus, and a squirrel (Table 8) are other species, which appear to have adopted this dispersal route and the same may explain discontinuous distributions of other forest mammals in the Central forest Regions (Misonne, 1963:87).

Dispersal of Montane Mammals

Montane mammal faunas in Africa still require adequate definition but do appear to be depauperate and hence derived. They show a strong degree of endemism, so that dispersal patterns are difficult to assess (Corbet and Yalden, 1972, and Yalden et al., 1976 for the Ethiopian Highlands; Rahm, 1965, and Kingdon, 1971, 1974*a*, 1974*b* for the Albertine Rift; Moreau, 1966, for distribution of montane "islands"). Distributions in East Africa are not inconsistent with Kingdon's (1971) concept of northern and southern dispersal routes. Recent dispersal between East Africa and the Ethiopian highlands has involved few species (*Lophuromys flavopunctatus, Otomys typus, Crocidura fumosa, Redunca fulvorufula*). The remarkable affinity between East African and Cameroon highland faunas is greater (*Myosorex* species, *Otomys tropicalis, Dendromus mesomelas, Cercopithecus lhoesti-preussi* superspecies, *Redunca fulvorufula*, and *Paraxerus cooperi* with *Funisciurus carruthersi*, if Kingdon, 1974*b*, should prove correct in regarding them as allospecies). Carcasson (1964), Moreau (1966), and Coetzee and Van Zinderen Bakker (1970) tried to explain analagous distributions in butterflies and birds by erecting a pluvial montane-forest bridge across central Africa, and were followed by Eisentraut (1973). However, montane forest did not even descend to the foot of East African mountains (Livingstone, 1975) let alone spread across the continent. It is more likely that, as Livingstone proposes, floristic changes in forest type concomitant with climatic changes created suitable transitory habitats for these mammals so that in cooler paleoclimatic phases, montane forest or, for that matter, non-forest biota may have dispersed into lowland environments more than at present. This happens today to some extent, as some highland forest species pen-

Table 6.—*Ancestor-descendant chains of subspecies or species, based on primitive and derived characters.*

1. Forest mammals; for key to symbols, see Fig. 1
   (a) *Cercopithecus (mitis) mitis* (EC, SC) → *C. (m.) albogularis* (E)
   (b) *Cercopithecus ascanius schmidti* (EC) → *C. a. whitesidei, ascanius* etc (SC); *C. cephus cephus* (WC) → *C. c. cephodes* (WC) → *C. erythrotis* (WC); *C. petaurista buttikoferi* (W) → *C. p. petaurista* (W)
   (c) *Cercopithecus campbelli* (W) → *C. mona* (Volta to Sanaga) → *C. denti* (EC) → *C. wolfi* (SC); *C. pogonias grayi* (WC) → *C. p. pogonias, nigripes* (WC)
   (d) *Cercopithecus preussi* (WC) → *C. lhoesti* (EC)
   (e) *Cercocebus agilis* (EC, WC) → *C. atys atys* (W) → *C. a. lunulatus* (W) → *C. torquatus* (WC)
   (f) *Colobus verus* (W) → *C. (badius) foae* (EC) → *C. (b.) badius* (WC)
   (g) *Colobus satanas* (WC) → *C. angolensis* (EC, SC) → *C. polykomos polykomos* (W) → *C. p. vellerosus* (W) → *C. guereza* (N. forest border to Ethiopia, Tanzania)
   (h) *Philantomba maxwelli* (W) → *P. monticola* (C, E)
   (i) *Cephalophus spadix* (E) → *C. silvicultor* (W, C)
   (j) *Neotragus pygmaeus* (W) → *N. batesi* (WC, EC) → *N. moschatus moschatus* (E) → *N. m. livingstonianus* (E)
2. Savanna and forest/savanna mammals; SS = Southern Savanna, NS = Northern Savanna, SA = Somali Arid, SWA = Southwest Arid
   (a) *Cercopithecus (aethiops) pygerythrus* → *C. (a.) aethiops* → *C. (a.) sabaeus*
   (b) *Papio cynocephalus* (SS) → *P. anubis* (NS) → *P. ursinus* (SWA); *P. papio* (NS) → *P. hamadryas* (SA)
   (c) *Xerus erythropus* (NS) → *X. inauris, X. princeps* (SWA)
   (d) *Cricetomys emini* (forest) → *C. gambianus ansorgei* (SS) → *C. g. gambianus* (NS)
   (e) *Procavia habessinica* and other northern *Procavia* spp. → *P. capensis, P. welwitschii* (SWA)
   (f) *Tragelaphus scriptus scriptus* (forest) → *T. s. ornatus* (SS) → *T. s. sylvaticus* (SS)
   (g) *Taurotragus derbianus* (NS) → *T. oryx* (SS)
   (h) *Syncerus caffer nanus* (forest) → *S. c. brachyceros* (NS) → *S. c. caffer* (NS, SS)
   (i) *Damaliscus korrigum* (NS), *D. lunatus* (SS) → *D. dorcas* (SS)
   (j) *Alcelaphus buselaphus tora, swaynei* (SA) → *A. b. cokei* (SA) → *A. b. buselaphus* (N. Africa) → *A. b. major* (NS) → *A. b. lelwel* (NS) → *A. b. caama* (SWA)
   (k) *Madoqua saltiana* (SA) → *M. kirkii* (SA, SWA) → *M. guentheri* (SA)
   (l) *Gazella soemerringi* (SA) → *G. granti* (SA)
   (m) *Equus grevyi* (SA) → *E. zebra* (SWA) → *E. burchelli* (SS) → *E. quagga* (SS)

Table 7.—*Hypothetical sequence of events in the speciation of* Colobus *monkeys.*

1. Dry Phase—*Colobus verus* in (West) Africa.
2. Moist Phase—*C. verus* disperses to Central Africa.
3. Dry—*C.* (*badius*) *foae* differentiates in E.C. refuge; acquires reddish pelage, greater sexual dimorphism; cephalic hair whorls diverge and are reduced.
4. Moist—*C.* (*b.*) *foai* disperses to West Africa.
5. Dry—*C.* (*b.*) *badius* differentiates in W. refuge; acquires blacker pelage, cephalic hair whorls lost.
6. Moist—*C.* (*b.*) *badius* disperses eastward to W.C. Forest Region.
7. Dry—*C. satanas* differentiates in W.C. Refuge; loses red pelage, acquires enlarged larynx, long mantle, pallid juvenile pelage (?).
8. Moist—*C. satanas* disperses to C. Regions.
9. Dry—*C. angolensis* differentiates in C. Regions; acquires white pelage, loses sexual swellings, becomes more tolerant of dry forest.
10. Moist—*C. angolensis* disperses to W. Region along route north of present forest boundary.
11. Dry—*C. polykomos* differentiates in W. Refuge—during an extreme dry period?
12. Moist—*C. polykomos* disperses eastward, principally along forest galleries.
13. Dry—*C. guereza* diverges in isolation as even more a species of dry forest (see Clutton-Brock, 1974).
14. Moist—*C. guereza* disperses widely into East Africa and Ethiopia during period which leads to present day.

etrate low latitude lowland forest (*Cercopithecus hamlyni* and *C. lhoesti* itself, Rahm, 1970) and other highland species descend to lowland forest at higher latitudes (Brain and Meester, 1964, for *Myosorex*, and Misonne, 1963, for *Otomys*).

Dispersal Direction

The direction of dispersal along a particular route is more difficult to assess than the route itself and inferences can be drawn only from the general faunistic premise that small faunas, especially if they lack endemics, are derivatives of larger ones, and from the study of primitive and derivative character states of species and subspecies. In a number of forest mammals, especially the primates, it is possible to identify sequences of successively more derivative subspecies or species, suggesting that a population has dispersed and formed a new isolate, which has itself given rise to another and so on, with each climatic cycle, so that a chain of ancestors and descendants are formed, which are yet contemporaries (Table 6). Schwarz's conclusions (1926*b*, 1928, 1929) were similar, though he did not always distinguish primitive and derived character states.

From Table 6 it is possible to interpret the speciation of colobus monkeys in terms of seven chief dispersals between the Western and Central Forest Regions in association with seven phases of isolation and differentiation (Table 7). The last putative eastward dispersal of colobus and the succeeding phase of isolation (commencing *ca.* 35,000 years BP?) can readily be related to inferred eastward dispersal in some other monkeys and a squirrel (Table 8). The hypothesis is based on Table 6 with extrapolation to other species where primitive-derivative character states are not yet identified, and is supported by certain zoogeographical details—for instance, none of the eastward-invasive animals have managed to reach Fernando Po, whereas the "resident" species are well represented there.

Booth (1958*b*) interpreted these sequences in Table 8 as "stepped clines" reflecting the breakup of more continuous populations in a series of Pleistocene refugia, of which he recognized two in the Western Forest Region to account for primate subspeciation there. He did not explain how the eastern subspecies are in some cases intermediate between the western one and derivative taxa occurring outside the Region (Table 6: b,e,g). A succession of isolations and dispersals provides, I think, a better explanation.

This hypothesis can be correlated with others concerning approximately contemporaneous evolutionary events—namely the derivation of the South-Central Forest Zone primates, speciation among West-Central Forest mammals (Table 5), or the concept of a dispersal corridor between Western and Central Forest north of present forest limits—to provide a preliminary reconstruction of recent forest faunistic history. Nevertheless, the level of supposition in the reconstruction remains very apparent.

Ecological Translation across the Forest-savanna Boundary

Direction in dispersal and speciation may be considered not only in a strictly geographic sense, but also from the ecological aspect. Most African mammals are probably confined to a major biome—forest, mesic savanna, arid savanna, or desert—though the extent to which this is true has not been critically examined (see distribution maps in Smithers, 1971; Schouteden, 1944–1946; Davis, 1974). The boundary between forest and savanna is a particularly clear one, and few species occur unequivocally in both habitats even though forest species

Table 8.—*Suggested eastward dispersal of western forest monkeys and a squirrel.*

Genera	Primary Western Refuge →	Secondary Refuge →	Nigeria, W of Niger River →	West-Central Region →	East-Central Region →	South-Central Region
Colobus	*p. polykomos*	*p. vellerosus*	*p. vellerosus*	*guereza*	*guereza*	
Cercocebus	*a. atys*	*a. lunulatus*	*torquatus*	*torquatus*		
Cercopithecus	*d. diana*	*d. roloway*				
Cercopithecus	*p. buttikoferi*	*p. petaurista*	*erythrogaster*			
Cercopithecus	*c. campbelli*	*c. lowei*	*mona*	*mona*	*denti*	*wolfi*
Colobus	*b. badius*	*b. waldroni*		*b. preussi*		
Funisciurus pyrrhopus	*lemniscatus* group	*lemniscatus* group	*raptorum* group	*raptorum* group	*akka* group	
Cercopithecus	*nictitans stampflii*					
Colobus	*verus*	*verus*		*verus*		

penetrate savanna along forest galleries and savanna species enter the forest when it is opened up by farms and roads (Rahm, 1972).

Successively stronger levels of differentiation between forest and savanna vicariants can be recognized in at least 30 superspecies and species-groups (Table 9). Leaving these species aside, there are still at least 26 genera, which include both forest and savanna species. When the distribution and taxonomy of these animals are better known, it will probably be possible to segregate some further evolutionary units as species groups or superspecies here as well. Five families whose species have not yet been considered, and another nine which already have, contain separate forest and savanna genera. A total of 28 families occurs in both biomes, as compared with three in the forest alone and 15, of which eight are rodents, only outside the forest.

The taxonomic levels of differentiation between forest and savanna mammals suggest there has been a long-term exchange between the faunas of the biomes through infraspecific dispersal from one to the other and eventually through speciation of vicariant populations, because eurytopic species occurring in both habitats are few.

Hypothetically, faunal exchange between biomes could be equally balanced, but the evidence, such as it is, suggests that it has been predominantly from forest to savanna.

Schwarz (1924) and Lonnberg (1929) believed that plains mammals had a forest origin, and Lonnberg indeed supposed that some of the savanna mammals of Africa had originated from the stranding of forest species during a long-term recession of the Great Hylea. Understandably, this explanation was rejected by Chapin (1932) and Moreau (1952) but its supporting evidence was not reinterpreted by either. Forest origins have been proposed or implied by various authors for Soricidae (Heim de Balsac and Lamotte, 1956, 1957), Cercopithecidae (Lonnberg, 1929; Napier, 1970), Procaviidae and Sciuridae (Lonnberg, 1929), Giraffidae (Harris, 1976), Bovidae (Estes, 1974), Nycteridae (Braestrup, 1935; Koopman, 1975), and Hystricidae (Kingdon, 1974*b*), while the most derived species in several of these families and in Manidae, Hippopotamidae, Suidae, Herpestinae (see Pocock, 1919; Taylor, 1974, 1976), and Felidae are clearly savanna taxa. These citations do not in themselves contribute evidence for a forest-savanna ecological translation, because the literature is diffuse and diverse, few authors having even considered the hypothesis' plausibility. The shortage of pan-African taxonomic studies and more especially of evolutionary studies partly explains this deficiency.

For families other than those mentioned above, no statement of forest origin has been made, nor can the original biome be regarded as self-evident, even though as in the case of the Pteropodidae, one is inclined to suspect it on zoogeographic grounds. Moreoever, some mammalian families (for example, Gerbillidae) have had a very long history of speciation in non-forest environments and may have originated there so that their ultimate ancestral habitat cannot readily be determined. Forest origins are accepted in interpreting the phylogeny of horse, elephant, or man, but proposals for forest origins in African mammals have not all remained undisputed. Thus, Kingdon (1971) regards the forest habitat as secondary in hyraxes, not noting contrary evidence presented by Lonnberg (1929) for a forest origin, and Lonnberg himself had to make a forest

Table 9.—*Mammalian taxa occurring in both forest and savanna.*

1. Species with weakly differentiated forest and savanna populations
    - *Crocidura occidentalis*
    - *Taphozous mauritianus*
    - *Hipposideros commersoni*
    - *Pipistrellus nanus*
    - *Heliosciurus gambianus*
    - *Mellivora capensis*
    - *Lutra macullicollis*
    - *Genetta pardina*
    - *Viverra civetta*
    - *Atilax paludinosus*
    - *Panthera pardus*
    - *Tragelaphus spekii*
2. Species with strongly differentiated forest and savanna subspecies
    - *Funisciurus congicus*
    - *Orycteropus afer*
    - *Loxodonta africana*
    - *Potamochoerus porcus*
    - *Tragelaphus scriptus*
    - *Syncerus caffer*
3. Superspecies with forest (listed first) and savanna allospecies
    - *Tadarida congica, T. trevori*
    - *Manis gigantea, M. temmincki*
    - *Aonyx congicus, A. capensis*
    - *Galago inustus, G. senegalensis*
    - *Paraxerus palliatus, P. cepapi, P. ochraceus*
    - *Cricetomys emini, C. gambianus*
    - *Manis gigantea, M. temmincki*
    - *Aonyx congicus, A. capensis*
4. Species groups with forest and savanna allospecies
    - *Hipposideros ruber, H. cafer*
    - *Rhinolophus alcyone, R. landeri*
    - *Heliosciurus gambianus, H. mutablis, H. rufobrachium*
    - *Thamnomys rutilans, T. cometes, T. dolichurus*
    - *Lemniscomys* species-complex
5. Genera with separate forest and savanna species
    - (a) Species additional to those already listed in the following genera
        - *Crocidura, Taphozous, Hipposideros, Pipistrellus, Rhinolophus, Galago, Genetta, Tragelaphus*
    - (b) Species in the following genera
        - *Sylvisorex, Epomops, Rousettus, Nycteris, Eptesicus, Glauconycteris, Scotophilus, Kerivoula, Myopterus, Tadarida, Cercopithecus, Dendromus, Aethomys, Praomys, Graphiurus, Bdeogale, Felis*
6. Families with different forest and savanna genera
    - Soricidae, Macroscelididae, Cercopithecidae, Pteropodidae, Sciuridae, Cricetomyidae, Muridae, including *Oenomys-Thamnomys* group, *Malacomys* group, *Acomys* group and *Arvicanthis* group, Procaviidae, Hystricidae, Hippopotamidae, Suidae, Giraffidae, Viverridae, Bovidae

habitat secondary for bovids, because he was mistakenly forced to believe that they had radiated outside the continent. Kortland's dehumanization hypothesis suggests a savanna origin for the chimpanzee (Kortland and Kooij, 1963; Kortland and Van Zon, 1968); Buettner-Janusch (1966:267) proposed a forest invasion by *Cercopithecus;* and Kingdon's (1971) speculation on *Galago* required speciation out of, but then back into, the forest. Misonne (1969) considers murids to be primarily savanna animals in Africa, yet he regards forest as a marginal refuge habitat (1969:167, 171) for certain more primitive species. From his conclusions, it seems quite possible that apart from the *Praomys* and *Mus* groups, all African murids could represent a single radiation within the Continent; there seems to be no very compelling reason for supposing that the occurrence of certain primitive genera and species in the forest should not indicate a forest origin for this radiation.

Few other statements to the effect that African forest mammals were derived from savanna species have been made. The problem of ultimate biome origin is nevertheless not an easy one to handle, for speciation across a major ecotone can be interpreted in several ways from primitive-derivative characters. With a colonist in biome B and its cotemporal primitive ancestor in biome A, there has been a dispersive speciation from A to B, but, if the ancestor is itself replaced in A by a third and even more advanced form, while the taxon in B retains primitive features, dispersal could be misinterpreted as having occurred from B to A. Animals like *Sylvicapra grimmia* and *Cercopithecus aethiops,* for example, retain very conservative color patterns and hair-banding characters, with respect to their congeners in the ancestral forest habitat, yet a wealth of evidence suggests that ecological drift in Bovidae and Cercopithecidae has indeed been from forest to savanna.

Evidence for relatively recent dispersal into the savanna by forest mammals comes from a study of certain eurytopic species or species groups occurring in both biomes. These mammals exhibit a morphological continuum between populations, yet have areas of parapatry, sympatry, or secondary intergradation between extreme phenotypes where demes have converged on each other in dispersing from different areas. Primitive characters occur in the forest populations, more derivative ones in the savanna, whereas the reverse is not usually evident.

The buffalo, *Syncerus caffer*, provides one of the best examples (Grubb, 1971, and in preparation), so great is the contrast between the forest and savanna forms and so clear are the derivative characters of the latter. This species and the elephant, *Loxodonta africana*, apparently dispersed into the savanna in West Africa and continued their dispersal through the Northern Savanna and around the forest block into Angola and South Africa. In East Africa, both replaced other species in the late Pleistocene—the more primitive *Homoioceros* and the more derivative *Elephas recki* (Maglio, 1973).

More species appear to have crossed the southern forest-savanna border, and in Angola there is clinal variation between forest and savanna populations of *Hipposideros* (*caffer* group, Koopman, 1975), *Cricetomys*, and *Heliosciurus*, which in other parts of Africa are sympatric. The *Hipposideros caffer* group, the giant rat *Cricetomys*, the bushbuck, *Tragelaphus scriptus*, and the bushpig, *Potamochoerus percus*, all have dispersed from the forest through the Southern Savanna northward into East Africa. The bushbuck did not reach farther than southern Sudan in this northward progression, other subspecies having colonized Ethiopia and the Northern Savanna, but the bushpig did get to the Ethiopian highlands. *Cricetomys gambianus* and *Hipposideros caffer* have spread farther, throughout the Northern Savanna, the latter coexisting with its forest congener *H. ruber* where this species penetrates savanna.

A third route has been adopted by the squirrel *Funisciurus congicus*. Species of this genus reach into the savanna along riverain forest (*F. pyrrhopus, F. anerythrus, F. substriatus, F. bayoni*) but *F. congicus* extends much further, from the forest of the Cuvette Central south through western Angola into the dry mopane woodland of South West Africa, in one continuous clinal sequence.

Speciation and Dispersal in Savanna and Arid Biomes

Endemism or vicariantism of non-forest mammals tends to be related to the two Savanna Zones or three Arid Zones of Davis (1962) with, for instance, *Taurotragus derbianus* in the Northern Savanna, *T. oryx* in the Southern, or *Oryx dammah* in the Sudanese, *O. beisa* in the Somali, *O. gazella* in the South West Arid (Ansell, 1972). These Zones have hence been centers of isolation, but it is unlikely that they were ever reduced to small refugia, contra Moreau (1966:98).

Other regions have had a less prominent role in speciation. In the Northern Savanna, a number of endemics are found only east (for example, *Helogale dybowskii*) or west (for example, *Genetta thierryi*) of the Lake Chad and Chari Basin area, whereas certain taxa are represented by divergent allospecies or subspecies in these regions (Schwarz, 1926*a*; Grubb, 1971; Groves, 1975). The Pleistocene lake Megachad may have been the instrumental barrier to dispersal here. A small faunal element is located in the Senegal area, including endemic semispecies (particularly *Papio papio* and *Sylvicapra grimmia coronata*) and isolates of otherwise widely distributed species. The factor encouraging isolation is not known. The Nile swamps and Ethiopian Highlands were probably also refuge centers for savanna mammals in arid periods.

In the Southern Savanna, the Muchinga scarp is involved in separating semispecies of baboons, blue monkeys, sun-squirrels, and waterbuck (Ansell, 1960) and may have accounted for speciation between roan and sable antelopes, for it lies central to their area of sympatry. The Rufiji basin (Kingdon, 1974*a*) and the Escarpment Zone of Angola (Cabral, 1966) have also been proposed as barriers promoting isolation in mammals, whereas others such as the Nyasa Rift were probably involved. Endemism in southern Africa is discussed by Rautenbach (1978) and speciation in *Elephantulus*, Otomyinae, and Chrysochloridae, for example, must have been complex in this part of the Continent. Speciation in Saharan mammals, particulary rodents, is perhaps best linked with evolutionary studies of the whole Eremian fauna. There is a complex situation in the Somali Arid Zone, with speciation or secondary contact among large- and small-nosed dikdik, giraffe, larger and smaller gazelles, hartebeest, and zebras (Keast, 1965). The mammals making up the famous East African Plains Fauna, which occurs within the Zone, are of diverse zoogeographical affinity and wildebeest, gazelle, and perhaps hartebeest and rhinoceros (see Brooks, 1961; Groves, 1967) have been influenced in their subspeciation by the Kenya Rift. The discontinuous distribution of species and superspecies in the Somali and South West Arid zones has been extensively discussed and explained by dispersal along a former Arid Corridor during a dry climatic phase (Benson and White, 1960; Ansell et al., 1962; Ansell, 1960; Bigalke, 1972). The dry-savanna mammals of the Rukwa valley and isolated populations of wildebeest, giraffe, and tsessebe in Zambia (Ansell, 1960) perhaps represent a vestige of this dispersal.

Dispersal directions are not always easily inferred in non-forest mammals but they may have involved complex patterns of replacement with very wideranging dispersal. For example, in their northern distributions, as well as in southern Africa, neither hartebeest nor baboons have their most closely allied allospecies in contact. The Ethiopian hartebeest, *tora*, is phylogenetically nearer the West African *major* or the extinct North African *buselaphus* than the very different Sudanese *lelwel* with which it forms a hybrid zone (Ruxton and Schwarz, 1929). And *Papio papio* of Gambia and Senegal is nearer *P. hamadryas* of Ethiopia and Somalia than *P. anubis* of the intervening Northern Savanna (Hill, 1970).

A notable problem is the absence of any indication of dispersal through Angola and Congo to the Central African Empire, where a route should have been available when forest was reduced to small refugia (see Carcasson, 1964; Hamilton, 1976). The significance of this has yet to be assessed.

A number of superspecies are not restricted to arid or savanna zones, but show more complex distribution patterns, with some allospecies in both mesic and arid zones and others in only one or the other. This group includes mammals where the Northern Savanna form is either restricted to the Guinea Savanna or is more eurytopic, reaching into the Sudanese Arid Zone, whereas the nearest ally is a stenotopic Southern Arid species. *Alcelaphus* (*buselaphus*) *lelwel, Papio anubis, Xerus erythropus,* and *Procavia latastei* in the Northern Savanna are represented by *A.* (*b.*) *caama, P. ursinus, X. inauris,* and *P. capensis* in the Southern Arid Zone, to which they are restricted. Related trends are seen in *Sylvicapra grimmia*, where derivative subspecies have penetrated the Southern Arid, yet conservative subspecies have not dispersed into the Sudanese Arid (Groves, personal communication), and the eland, where the primitive *Taurotragus derbianus* is restricted to Guinea savanna, yet the derivative *T. oryx* is much more habitat-tolerant and extends into the Kalahari. The giraffe, white rhinoceros, and hedgehog are also in part more ecologically restricted in their southern distributions.

These distribution patterns suggest an ecological translation from mesic to arid habitats, a view supported by the derivative character of all the Southern Arid allospecies (Table 6). Other Southern Arid or Grassland species (*Oryx gazella, Antidorcas marsupialis, Damaliscus dorcas, Connochaetes gnou, Phacochoerus aethiopicus aethiopicus, Equus quagga*) are also derivative. And the paucity and strongly derivative adaptations of desert mammals suggest that they too have originated from other habitats.

Ecological Direction in Dispersive Speciation

From this discussion and earlier remarks about forest origins of savanna species, it would appear that if speciation involves an ecological translation from one biome to another, then it is predominantly from mesic, predictable and less seasonal habitats toward arid, less predictable and more seasonal environments, and hence involves a descent of the species-diversity gradient. The slope of this gradient in Africa is considerable; it is best measured in areas where habitats are clearly stratified, as in West Africa. Rosevear (1949) presents data from which it can be calculated. The gradient in number of mammal species per biome is 130, 60, 47, 37 from forest through Guinea, Sudan, and Sahel savannas in Nigeria. These data are provisional; I obtain 141, 106, 86, 49 and 22 (desert) for the same transect west of the Volta River. Implications for theories of faunal steady states (MacArthur, 1972:174; Rozenzweig, 1975), or faunal exchange (Wilson, 1965) arise if dispersive speciation is indeed predominantly unidirectional along this gradient, and the possibility that biomes are faunistically imbalanced necessarily follows.

CONCLUSION

An important impediment to the reconstruction of speciation in African mammals is the scarcity of taxa with apparently significant and interpretable geographic variation and dispersion. It is impossible to recognize centers of dispersal or refugia when variation is clinal and low-key, and it is impossible to trace any dispersal track when primitive-derivative characters have not been recognized. And these may be misleading, in suggesting a dispersal direction opposite to the one which occurred. There is in any case some danger in assuming that primitive-derivative morphological series always represent ancestors and descendants, though this may be nearer the truth and at least no more mistaken than suggesting that two contemporaries share an extinct common ancestor that was phenetically equidistant between them. However, in many cases, the temporal divergence in morphology that does occur between primitive and derivative stocks once gene flow between them has ceased must now obscure the relationship.

Very few reconstructions of species histories are likely to be possible, therefore, even with the degree of surmise entailed in the *Colobus* model (Table 7). The absolute time span involved in a case like this is hard to assess, for we do not know what scale of paleoclimatic events were needed to drive the isolation-dispersal system, and therefore whether speciation took a longer or shorter time. Even relative time-scaling presents problems. Taxa that have diverged to different degrees, for instance, may have speciated at different rates or over different periods of time, and there may now be no way of distinguishing such equally parsimonious hypotheses. Even with a single superspecies, events may get telescoped—a succession of divergences may be regarded as cotemporal (Booth, 1958*b*).

What we clearly need are more evolutionary data for developing more rigorous models of speciation. We may expect further paleontological studies to do this for the larger mammals and karyological work for the smaller species, as it has already contributed so much outside Africa. Logistic problems may allow faunistic and taxonomic studies to hold sway for some time and we certainly need many more accurate distribution maps. The classification of distributions is an important first step in reconstructing faunal histories. Some of the hypotheses presented in this paper are supported by evidence from African birds, reptiles, and butterflies and a less sectarian approach may in the future prove more productive.

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THE DAHOMEY GAP—A REEVALUATION OF ITS SIGNIFICANCE AS A FAUNAL BARRIER TO WEST AFRICAN HIGH FOREST MAMMALS

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ABSTRACT

The Dahomey Gap as a faunal barrier to high forest mammals is reevaluated. Past researchers, utilizing incorrect or incomplete data, were led to the conclusion that the Gap was the major factor influencing high forest animal distribution in West Africa. Recent data on climate, vegetation, soil type, and mammalian taxonomy, ecology, and distribution indicate that the Dahomey Gap has not influenced mammal distribution or evolutionary changes. Rather, it is the Volta and Niger rivers, which have affected mammalian distribution and speciation in West Africa.

INTRODUCTION

The Dahomey Gap, as an ecogeographical barrier to high forest animals, has been discussed by many authors including Booth (1954, 1958*a*, 1958*b*) and Dekeyser (1955) for mammals, Clausen (1964) for fishes, Schiotz (1967) for tree frogs, and Moreau (1969) in his synopsis of the origin and effects of this barrier. Mammals collected recently from isolated patches of high forest within the Gap suggested that there was no barrier. Prior to this analysis the only faunal data available were from the forests bordering the western and eastern limits of the Gap.

The collections (1967–1968) of mammals made by the Smithsonian African Mammal Project under the direction of H. W. Setzer, from the forest of southeastern Ghana, the forest of southwestern Nigeria, and particularly the southern parts of Togo and Dahomey (=Benin) (see Robbins, 1978, for Togo and Dahomey bats); and collections in Togo by the Laboratoire de Zoologie du Rijksuniversitair Centrum van Antwerpen in conjunction with the Musee Royal de l'Afrique Centrale (in Tervuren, Belgium) (for additional Togo bats see DeVree, DeRoo, and Verheyen, 1969; DeVree, Hulselmans, and Verheyen, 1970; and DeVree and Van der Straeten, 1971), provide new information on the ecogeographical significance of the Dahomey Gap.

The presence of high forest mammals within the Dahomey Gap necessitates a reevaluation of the following points.

1) On vegetation maps of Africa, a prominent feature is the division of the evergreen forests of West Africa into eastern and western parts—the Upper Guinea Forest (Guinea Forest block), which extends from the Volta River in Ghana west to Guinea, and the Lower Guinea Forest (Congo Forest block), which extends from southwestern Nigeria, across southern Nigeria, and east to Gabon and Zaire. The area between is commonly known as the Dahomey Gap (Moreau, 1969). The so-called Dahomey Gap is therefore an irregular area which takes in the southern parts of Togo and Dahomey, and southeastern Ghana (Clausen, 1964). Fig. 1 shows the major vegetation zones in the area under consideration in this report.

2) Within the Gap the savanna vegetation, which characterizes the West African interior, extends south to the Gulf of Guinea (Clausen, 1964).

3) The southern parts of the Gap, especially in Togo and Ghana, are in fact amazingly arid, generally resembling the Sudan Savanna in climate and vegetation (Clausen, 1964).

4) About half of the width of the Gap is occupied by a forest-savanna mosaic in the form of a strip bordering each forest block. Within this mosaic the forest patches are evidently small today. The central 100 mi of the Gap is a humid savanna (Moreau, 1969).

5) Some descriptions (Dekeyser, 1955; Booth, 1958*b*) claim that the Gap could be defined as a forest relict and may not be a formidable barrier. Moreau (1969) suggests that this may refer to the zone between the Volta River and the Togo highlands as having forest patches.

6) For forest animals the Dahomey Gap would be expected to form an important barrier that would result in evolutionary divergence at its two edges (Moreau, 1969).

7) Moreau (1969) reported that Schiotz (1967) found no forest animals in the forest patches within the Gap.

8) The limits of the forest and the forest-savanna

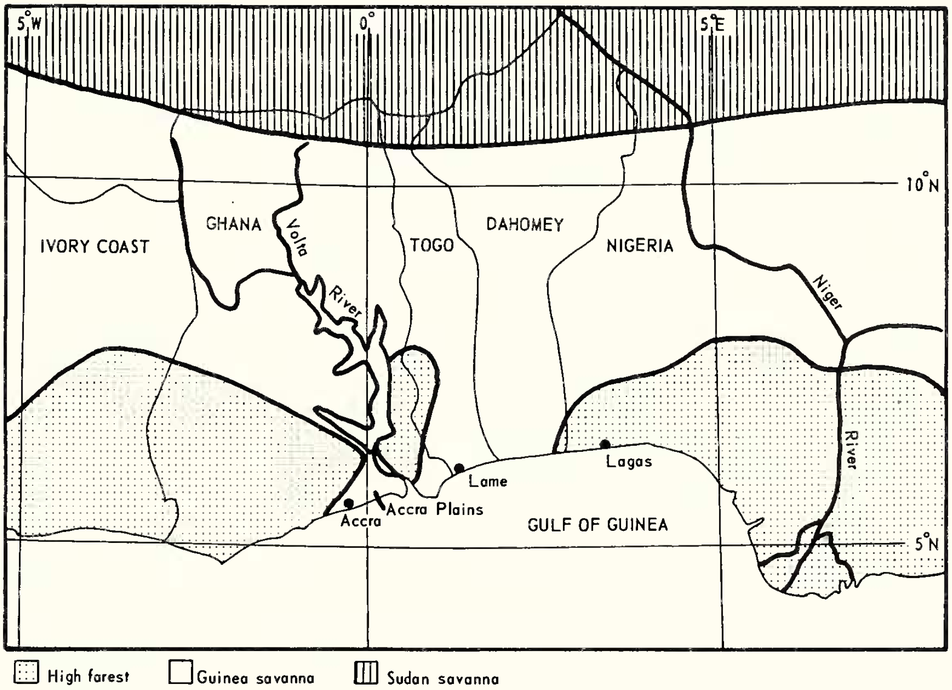

Fig. 1.—Major vegetation zones in West Africa.

mosaic do not seem to conform closely to the rainfall isohyets (Moreau, 1969).

9) The mammal distribution data examined by Booth (1958*b*) suggested to him that the Niger and the Volta rivers form the most important zoogeographical barriers in present-day West Africa. The Dahomey Gap in its present form is of less importance, but in the past must have had a considerable influence on the differentiation of the fauna east of the Niger and west of the Volta (Booth, 1958*b*).

10) A break in the forest approximating the location of the Dahomey Gap has been present for the last 10,000 years, prior to which time the Upper and Lower Guinea forests were united for at least an equal period (Moreau, 1969).

11) D. E. Livingstone (personal communication, 1977) said it was reasonable to accept the Dahomey Gap as a barrier, probably dating in its present form from about 5,000 years ago. He believes that most of that time breaks in continuous forest vegetation probably were few and of short duration until human interference changed the landscape.

12) The climatic picture is one of drought for some few thousand years prior to 12,000 BP; increased rainfall, especially between 10,000 and 5,000 BP; and a reversion to a more arid climate since about 5,000 BP (D. E. Livingstone, personal communication, 1977).

This paper presents an analysis of the effects of the Dahomey Gap based on recent climate, vegetation, soil type, and mammal distribution data. The evidence presented here contradicts the data and conclusions of Moreau (1969). He presented data, which established the Dahomey Gap as the major faunal barrier in West Africa. Apparently he drew his conclusions about 10 years too soon. Moreau (1969) admitted that his evidence was puzzling and contradictory. This may be because he used information extrapolated from East African climatic history to West Africa, which was either not pertinent or incorrect, and also before the taxonomy, distribution, and ecology of high forest animals were better known.

DISCUSSION AND RESULTS

Vegetation and Climate

Vegetation characteristics in equatorial tropical Africa are dependent on several factors. Among these are climate and soil type. Rosevear (1965) characterizes the high forest in West Africa as a distinguishable vegetation zone requiring at least

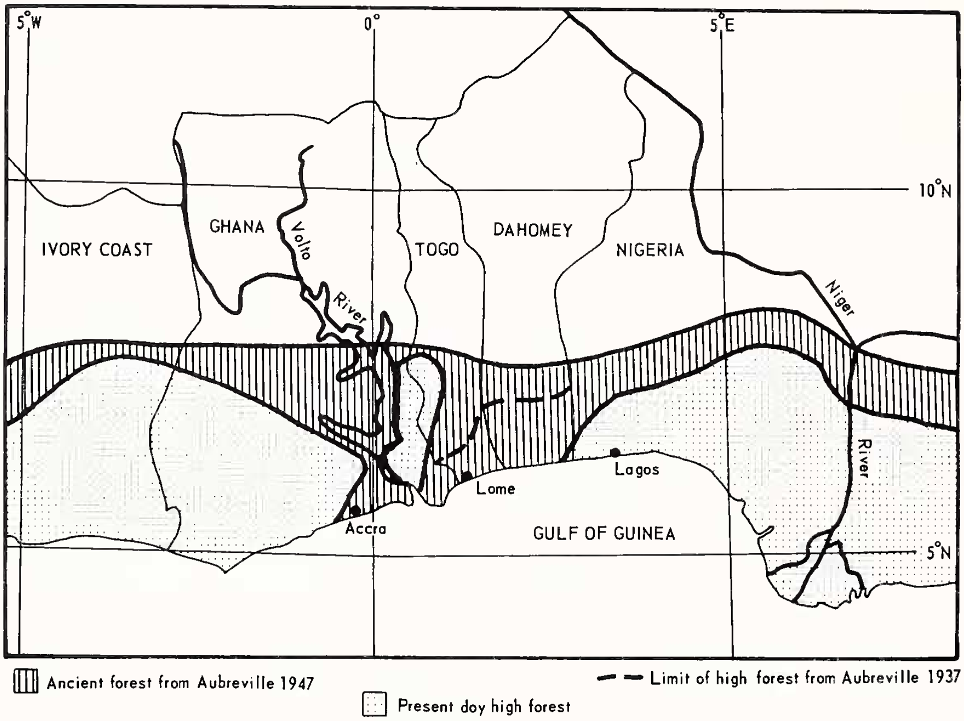

Fig. 2.—Present-day and ancient high forest zones in West Africa.

200 cm of rainfall annually. As Moreau (1969) points out, the limits of the forest do not conform closely to the rainfall isohyets. Because of this, other factors must be considered to determine the effectiveness of the annual total rainfall on the distribution of high forest vegetation. Temperature, relative humidity, air movement, soil condition, drainage, and topography are some of those factors (Richards, 1966).

One or several of these factors must be different (see Aubreville, 1949) if the climate and vegetation of the Dahomey Gap differs from the forests to the east and west, by being more arid and resembling the savanna (Clausen, 1964). Livingstone (1975) and others report climatic changes in Africa during the Quaternary. The Dahomey Gap area would have been at times a savanna bounded on both sides by high forest, at other times a part of a continuous forest, and at other times a part of a more widespread coastal savanna.

The zoogeographical data Moreau (1969) presented would seem logical if the Dahomey Gap existed in the form of a savanna for the past 10,000 years. However, following Livingstone (1975, personal communication, 1977), with a change to a more arid climate beginning about 5,000 BP, the following statements on vegetation and mammals become more meaningful.

The forest-savanna mosaic, also termed derived savanna, contains patches of high forest vegetation not confined to streams. It is generally agreed that this zone (which includes the Dahomey Gap area) has been covered with high forest in the past (the ancient forest) and that it is the influence of man that has transformed these areas into savanna (Schiotz, 1967). The derived savanna area has microclimatic patterns characteristic of the savanna influenced by changes in the vegetation cover (Schiotz, 1967).

The first major study of high forest characteristics and origins in the Dahomey Gap area was by Aubreville (1937). That study indicated that during the early 1900's there were still vestiges of an ancient forest in Togo and Dahomey. He experienced forest clearings for agricultural purposes throughout the area. Also, he stated that if the disappearance of the forest was of an old happening, then the forest patches would be long gone. His analysis of the species composition of those forest patches indicated that they were the same as the large bordering equatorial forest blocks.

Aubreville (1937) traveled throughout the area of

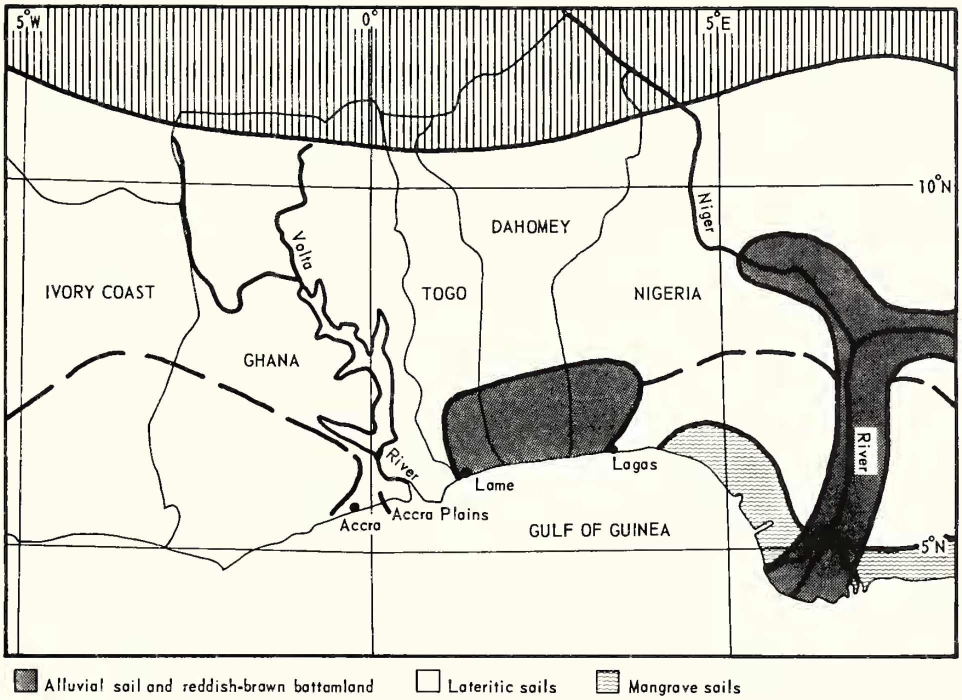

Fig. 3.—Major soil types in West Africa.

the Dahomey Gap exploring for evidence to determine the northern limit of the ancient coastal forest. He determined that it was up to 60 to 80 km from the coast in Dahomey and 40 km in Togo. In a later paper (Aubreville, 1949), the area occupied by the ancient forest was enlarged (Fig. 2). His evidence was the persistence of species of large trees known to occur only in the equatorial high forest. Although the destruction of the forest was extensive at the time of Aubreville, my examination of ERTS-1 (taken in 1973) and LANDSAT-2 (taken in 1976) satellite photographs in conjunction with first hand observations (in 1968), shows the presence of isolated patches of high forest still present within the Dahomey Gap area.

The humid tropical and equatorial high forest zones of Africa are usually characterized by lateritic soil types. The term laterite may be applied to the end result of a process, which preferentially leaches silica from the substrate. The end result is a soil having a mixture of alumina and iron oxides with very little else (Richards, 1966). Lateritic soils are also characterized by a low nutrient and organic content, with resulting low fertility. However, this soil readily supports the tropical high forest because of continuous nutrient recycling (FitzPatrick, 1971). When high forest vegetation is eliminated in agricultural practices the fertility of the soil is quickly exhausted and crop failure results. This may account for the shifting of cultivated areas in high forest zones (FitzPatrick, 1971). After vegetation removal, plant succession back to the high forest community with subsquent soil nutrient regeneration, can take from 20 years to a century or more (Richards, 1966).

However, a different soil type occurs in the Dahomey Gap area between Lome, Togo, and Lagos, Nigeria. This area is composed of alluvial soils (sands) and reddish-brown bottomland (The Atlas of Africa, 1973; Fig. 3). These soils probably have a high nutrient and organic content. Climatic conditions are such that left undisturbed, this area would support typical high forest vegetation. Because of the high nutrient and organic content of the soil, continued land use for agriculture is possible after the high forest is removed. This type of continual land use would result in what Richards (1966) calls a "deflected succession." This means a shifting of the biotic climax to resemble other climatic climaxes, though not the rain forest from which they were derived (Richards, 1966). In the area of the Dahomey Gap this "deflected succession" is culminated in the replacement of the high forest by open grassland, which may be called de-

Table 1.—*Mammalian taxa which occur from west of the Volta River to east of the Niger River.*

Scotonycteris zenkeri
Scotonycteris ophiodon
Hypsignathus monstrosus
Nanonycteris veldkampi
Myonycteris torquata
Megaloglossus woermanni
Taphozous peli
Nycteris grandis
Nycteris argae
Hipposideros cyclops
Hipposideros fuliginosus
Pipistrellus nanus
Mimetillus moloneyi
Chalinolobus poensis
Cercopithecus nictitans martini
Idiurus macrotis cansdalei
Anomalurus beecrofti
Anomalurus derbianus
Atheurus africanus
Hybomys univittatus
Lophuromys sikapusi
Malacomys longipes
Hylomyscus sp.
Praomys sp.
Thamnomys rutilans
Graphiurus hueti
Funisciurus leucogenys
Funisciurus substriatus

Table 3.—*Mammalian taxa which occur from the Niger River to the east.*

Epomops franqueti franqueti
Arctocebus calabarensis
Galago alleni
Galago crassicaudatus
Galago demidovi murinus
Perodicticus potto juju
Cercopithecus erythrogaster
Potamochoerus porcus pictus
Dendrohyrax dorsalis nigricans

rived savanna, and can be maintained as a biotic climax. This has led to recurrent statements in the literature by many authors implying that the Dahomey Gap is a natural savanna extension to the coast between two major forest blocks. In fact it is an area modified by man, which would normally be covered by high forest and is probably no older than the advent of man practicing intensive agriculture.

The limit of the Dahomey Gap given by Booth (1958*b*), Clausen (1964), and Moreau (1969) is between the Volta River in eastern Ghana and southwestern Nigeria. Clausen (1964) also apparently included the Accra Plains in southeastern Ghana, which extended the Gap west of the Volta River. For the purposes of this report the Accra Plains, being a unique area vegetationally and not a part of the Lower Guinea Forest block, and because high forest vegetation and animals are found between the Volta River and continuing into the western Togo highlands, the Dahomey Gap is considered to lie between the western Togo highlands and southwestern Nigeria.

Table 2.—*Mammalian taxa which occur from the Volta River to the west.*

Hipposideros jonesi
Colobus waldroni
Colobus verus
Cercopithecus campbelli
Cercopithecus diana roloway
Anomalurus peli
Hybomys trivirgatus
Heliosciurus rufobrachium maculatus
Protoxerus aubinni
Epixerus ebii

Mammalian Fauna

Many of the major vertebrate groups have been examined with reference to distribution and effects of the Dahomey Gap. Marchant (1954) examined birds; Clausen (1964) cyprinodont fishes; Schiotz (1967) tree frogs; and Booth (1954, 1958*a*, 1958*b*) primates and most other mammalian orders. These data provided the faunal information used by Moreau (1969) in his examination of the physical and ecological faunal barriers in West Africa.

Moreau (1969) chose not to supplement the above studies with other data. He believed (correctly) that compilations from general check lists with imprecise taxonomy and ecology would not be useful. His report states (p. 40) ". . . defective though the available data are, there is no doubt that in sum they provide a basis for valid discussion of an exceedingly interesting situation."

Table 4.—*Mammalian taxa which occur from the Niger River to the west.*

Epomops franqueti strepitans
Perodicticus potto potto
Galago demidovi demidovi
Colobus polykomos vellerosus
Cercopithecus petaurista petaurista
Malacomys edwardsi
Dendrohyrax dorsalis sylvestris
Potamochoerus porcus porcus
Cephalophus maxwelli
Cephalophus niger

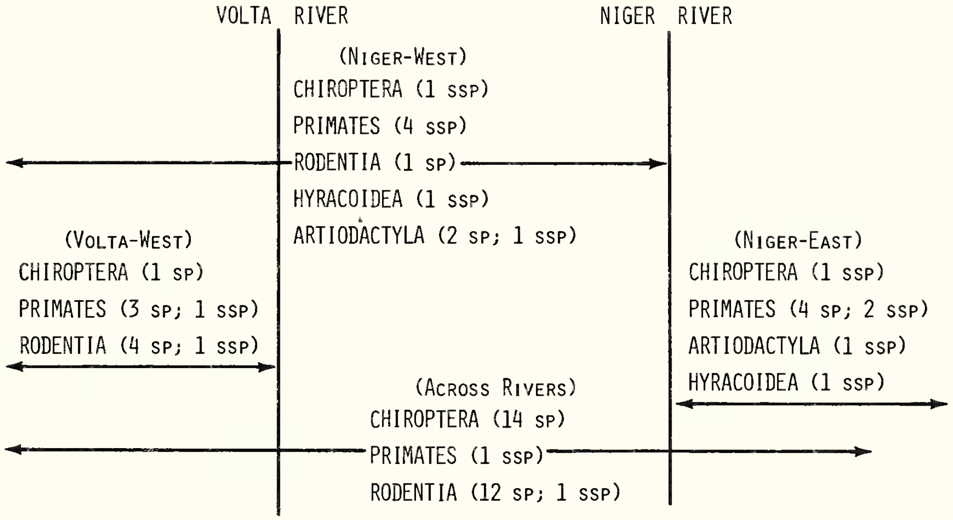

Fig. 4.—Mammalian taxa changes by order for the four major distributional categories.

One problem that becomes evident on examination of the previous reports on birds, fishes, tree frogs, and mammals, is that they were not collected within the area of the Dahomey Gap. As mentioned in the introduction, mammal specimens are now available from the Dahomey Gap as well as additional specimens from areas west and east of the Gap. Also, many of the major mammalian groups have been studied so that information on their taxonomy and ecology is available and compiled in a series edited by Meester and Setzer (1971).

Moreau (1969) discussed the influence of three topographical features as faunal boundaries—the Lower Niger River, the Dahomey Gap, and the Baoule V/Bandama River. Booth (1958*b*) also included the Volta River as a faunal barrier. To assess the possible influence of the Dahomey Gap on West African high forest mammalian fauna, taxonomy and ecology of mammals occurring from Nigeria west through Ivory Coast were studied. The mammal species and/or subspecies were divided into four categories.

The categories include taxa which occur (1) across the whole area under consideration (that is, across both rivers), (2) only west of the Volta River, (3) only east of the Niger River, and (4) only west of the Niger River. Three other categories were originally considered: taxa occurring only between the two rivers; those occurring only east of the Volta River; and those occurring from the western edge of the Gap and continuing westward. High forest

Table 5.—*Influence of the major river barriers.*

Major river barriers	Species changes		Subspecies changes	
	N	Percent	N	Percent
Across Rivers	26	45.6	2	3.5
Volta—West	8	14.0	2	3.5
Niger—East	5	8.8	4	7.0
Niger—West	3	5.3	7	12.3
Totals	42	73.7	15	26.3

Percent of Influence

Niger = 33.4
Volta = 17.5
Across Rivers = 49.1
100.0

Table 6.—*Mammalian taxa found in the Dahomey Gap forest patches.*

Epomops franqueti strepitans
Myonycteris torquata
Megaloglossus woermanni
Hipposideros cyclops
Pipistrellus nanus
Chalinolobus poensis
Perodicticus potto potto
Galago demidovi demidovi
Cercopithecus petaurista petaurista
Cercopithecus nictitans martini
Cercopithecus mona
Protoxerus stangeri nigeriae
Funisciurus leucogenys
Funisciurus pyrrhopus nigrensis
Lophuromys sikapusi
Hylomyscus sp.
Praomys sp.
Cephalophus maxwelli

taxa in these latter three categories comprise only 8% of the total, so were excluded from the percent of taxa different in each of the four main categories.

Tables 1–4 list the taxa, which have been included in each of the four categories. Table 5 consolidates these four tables and gives the number of taxa in each category and percent of the total. It is divided to reflect species or subspecies change. These results are summarized in Fig. 4 with the number of taxa in each of the five mammalian orders in the four categories.

These data show that of the 57 taxa examined, 49.1% occur in both the Upper and Lower Guinea forests and their distribution is not affected by the Volta River, the Dahomey Gap, nor the Niger River. Of the remaining taxa (50.9%), 33.4% are influenced by the Niger River. The Niger seems almost equally effective in limiting distribution of mammal taxa occurring east of the river (15.8%) and those occurring west of the river (17.6%). In contrast, the Volta River primarily restricts the distribution of taxa, which occur to the west (17.5%). Of the species occurring east of the Volta only one (*Cercopithecus mona*) does not cross, whereas one has a subspecies boundary at the Volta with *Heliosciurus rufobrachium isabellinus* occurring east of the river and *H. r. maculatus* occurring west of the river.

The Dahomey Gap forest patches contain 18 species of mammals (Table 6). Of these taxa, 10 occur across both rivers, five from the Niger to the west, two from the Volta to the east, and one occurs only between the two rivers.

It is apparent from these data that contrary to previous reports, the Dahomey Gap has had little influence as a faunal barrier on the distribution of high forest mammals in West Africa. In contrast, both the Volta and Niger rivers have been major factors influencing mammal distribution, with the Niger being the more important (33.4% as opposed to 17.5% for the Volta). It is possible that the Akosombo Dam on the Volta and the resulting large Volta Lake will further restrict distribution to the north of the dam and allow greater ease of crossing the river to the south of the dam. In any case, land use, which results in forest destruction in the Dahomey Gap area, with its different soil type, may result in a Gap, which may play an important role in future speciation and distribution of West African high forest mammals.

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A NUMERICAL RE-APPRAISAL OF THE SOUTHERN AFRICAN BIOTIC ZONES

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ABSTRACT

The acceptability and credibility of the empirically derived biotic zones of southern Africa are mathematically tested by means of Duellman's (1965) Faunal Resemblance Factor analysis. The distribution of 275 southern African mammalian species is analyzed. A total of six biotic zones, including three that were formerly regarded as subzones, are found to be viable biogeographic entities of full zonal status.

INTRODUCTION

Zoogeography has been defined as ". . . the scientific study of the distribution of animals on earth . . ." (Udvardy, 1969:1). Through the years a number of attempts have been made to classify animal life into meaningful distributional units, and the field has been subdivided in diverse ways toward different ends. Perhaps the suggested subdivision most pertinent to this paper is that proposed by Darlington (1957:11), who distinguishes three possible levels of approach: 1) geographical distribution over the entire earth; 2) regional distribution over selected segments of the earth; 3) local distribution, including species geography ("the geographical distribution of species in relation to each other and to ecology and evolution").

This study will consider a statistical analysis of the distributional trends of southern African mammals, in an effort to reevaluate the validity and credibility of the empirically derived biotic zones of the southern subcontinent. It is primarily aimed at the second level of Darlington's zoogeographical approach, and deals with the regional distribution of the mammals of southern Africa. Unfortunately regional studies such as this are often bound to political, rather than natural, areas.

Udvardy (1969:6) distinguishes static faunistic and regional zoogeography from dynamic causal zoogeography. He furthermore distinguishes specifically between zoogeography and ecology. Zoogeography in its purest sense concerns itself with the reasons for the arrival and settling of a species in a certain area. A study of why and how a species is able to live in that particular area is an ecological problem. Similarly, Simpson (1965:71–73) recognizes three levels of zoogeography—geographical, ecological, and historical. Both the zoogeographical and ecological attributes of distribution are the product of evolutionary processes during the course of time; hence, truly explanatory models can only be framed on a historical basis.

An accurate and detailed knowledge of subspeciation is essential in most modern computations aimed at causal zoogeography. The reverse is, however, also true; a consideration of the biogeography of taxa is important when studying subspeciation. Zoogeography and taxonomy are thus interdependent. The subspecific status of the majority of southern African mammals is, in the modern context, unsatisfactorily resolved, and thus severely hampers any detailed and accurate biogeographical analysis. Available analytical procedures based on subspeciation have therefore not been considered in this study pending further detailed survey work and subsequent taxonomic studies on the subspecies level. Consequently, this study is essentially limited to Udvardy's static faunistic and regional zoogeographical approach, and is thus primarily ecological in context.

The major biogeographical zones or provinces currently accepted for Africa stem from Sclater (1896). He subdivided Africa into four subregions—the Sahara, West Africa, Cape, and Malagasy. Recently, the Malagasy subregion was upgraded to regional status (Darlington, 1957). Hence the current concept of the Ethiopian region is Africa south of the Sahara.

Chapin (1923, 1932), working on the avifauna of Zaire (formerly Belgian Congo), combined former approaches (Wallace, 1876; Sclater, 1896; Reichenow, 1900; Sharpe, 1893) with his own knowledge of the birds of tropical Africa. He divided Zaire into distinct avifaunal regions, which he based on vegetation types best fitting the distribution of birds. Chapin then attempted to follow these avifaunal regions into adjacent countries, eventually arriving at a subdivision of the Ethiopian region into biogeographical districts. His West African subregion, as well as his East and South African subregions, correspond closely to the subregions of Sclater (1896). Both approaches were essentially aimed at a broad separation of tropical forests from savannas and deserts.

In Chapin's (1932) treatise of Africa, southern Africa was subdivided into only two faunal districts—an eastern and a western-arid district. Chapin's work was soon accepted (see Bates, 1924; Lynes, 1924). However, Chapin (1932) himself comments that the least satisfactory portion of his zoogeographical map of Africa is the southern African district. He considers further subdivision necessary here, especially in order to accommodate the highveld grassland and the woodland savanna, as well as tropical montane and coastal forests.

Moreau (1952) collates and critically discusses the Tertiary geology and climate of Africa. In this light, he analyzes the distribution of passerine avifauna of Africa, firstly by biomes, and secondly with respect to its affinities with the avifaunas of Europe and Asia. He geographically subdivides these main biomes into smaller biotic zones. He considers affinities both on generic and specific levels, and found differences between these derived biotic zones to be great.

With regard to southern Africa, Moreau (1952) retains Chapin's (1923) South West Arid district more or less unaltered, as a biotic zone. However, Moreau introduces the concept of the Southern Savanna biotic zone, which combines Chapin's eastern, climatically moderate, woodland districts. As suggested by Chapin (1932), Moreau now also recognizes montane forests as distinct on a biotic zone level. He furthermore recognizes the small, but floristically very rich and distinct winter rainfall area around Cape Town, with its Mediterranean climate, as a separate biotic zone.

Moreau (1952) uses both the terms "biotic zone" and "biome." The first term has a definite zoogeographical connotation, the second ecological. According to Smith (1966), the biotic province (zone) concept ". . . embraces a continuous geographic area that contains ecological associations distinguishable from those of adjacent provinces (zones), especially at the species and subspecies level . . . ." The biome, on the other hand, is a major ecosystem, and is seen by Smith as ". . . a broad ecological unit characterized by the distinctive life forms of the climax species, plant or animal . . . ." Southern African biotic zones can in reality also be seen as biomes, except that as such they are only parts of the major biomes of Africa. Whatever the case, Moreau can be credited to be one of the first to employ the correct terminology in an African zoogeographical treatise, with consideration to concepts and terms developed in related fields such as ecology. This distinction between "biotic zone" and "biome" is recognized and applied in this report.

Davis (1962) employs the southern African portion of Moreau's (1952) biogeographical map in an analysis of distribution patterns of the local Muridae. He agrees with Moreau in the validity of the South Western Cape as a biotic zone. However, Davis' (1962) main zoogeographical contribution lies in the fact that for the first time the biotic zones, which were founded on avifaunal distributional data, are analyzed from a mammalian point of view, albeit on only one family. Davis slightly alters the borders of the biotic zones to conform with the vegetation map of Keay (1959).

In a discussion of the origins of the southern African mammalian fauna, Meester (1965) accepts Davis' modified version of Moreau's biotic zones. Although Davis' generalized attempts to subdivide the biotic zones went unnoticed, Meester's definite recognition of the Namib as a subzone of the South West Arid, and the Grassland as a subzone of the Southern Savanna, was soon accepted. This approach to the recognition of biotic zones is even more compatible with the biome concept.

There are other proposed systems for subdividing the subcontinent into major biogeographic units, especially those of Liversidge (1962) and Winterbottom (1962). However, the biotic zone concept as outlined above has become commonly accepted as relevant from an ecological viewpoint, especially with regard to higher vertebrates. It is also, to my knowledge, the only zoogeographical system considered in recent years for work on mammal distribution (see Davis, 1962; Meester, 1965). It is therefore appropriate that biotic zones should receive closer scrutiny here, especially because no less than four currently recognized major biotic zones (two with two subzones each) are represented in southern Africa. Meester's (1965) refined version of Moreau's (1952) biotic zones is analyzed in this report.

METHODS

The African biotic zones and subzones have been empirically derived by considering main vegetation types and how they best fit the distribution of species, initially of birds and later of mammals. The zones are thus largely subjective. A number of species may be confined to a single biotic zone (endemics), but very few have ranges coinciding entirely with the boundaries of the particular zone in which they occur. Generally their ranges are more restricted. Such endemic species are few in number, yet serve as the main argument to justify the recognition of the biotic zone. The majority of species occurs over several biotic zones, because the distributions are limited by factors more generalized than those governing the vegetation types on which the biotic zones are primarily based. These widespread species apparently formerly served no role in justifying the recognition of biotic zones.

Duellman (1965:677) proposes a statistical analysis to express the validity of biogeographical subdivisions, based on the known distribution of all species in the entire area. He termed it the "Faunal Resemblance Factor," which is statistically expressed as $FRF = 2C/N1 + N2$, where C equals the number of species in common between the two zones compared, N1 equals the number of species in the first zone, and N2 equals the number of species in the second zone. An index value of 0.000 would indicate no taxonomic resemblance between two zonal faunas, and an index of 1.000 would indicate complete identity. A value of 0.500 would indicate that one-half of the species in each of the two zonal faunas are held in common, provided that they are of equal size. In the case of unequal-sized faunas, both dissimilarity in species composition and relative equality in species density are expressed. Duellman's (1965) formula is a simplified, yet equally effective, derivate of the Burt coefficient (Burt, 1958). Both formulas take the average of the two samples as the denominator (contrary to the Simpson and Jaccard coefficients, see Simpson, 1960), in an effort to reduce the effect of difference in size between them. However, the influence of differential faunal sizes is not entirely eliminated, and is yet another factor expressing similarity or dissimilarity between zones. These formulas are furthermore designed for taxa of which the geographical distributions of species are not well known. Only the presence or absence of taxa is of great importance. The Duellman coefficient is therefore ideally suited for this analysis, and was decided upon as being the simplest of the two mentioned here.

RESULTS

The distributions of 275 species of southern African mammals are given in Table 1. This list was compiled from updated but unpublished distribution maps kept in the Transvaal Museum for curatorial purposes, as well as from the literature, particularly Smithers (1971), Meester and Setzer (1971–1977), Davis (1974), Pringle (1974), Lynch (1975), and Smithers and Lobao Tello (1976). The taxonomic treatise of Meester and Setzer (1971) was followed. In the calculation of FRF indices, the Southern Savanna Grassland and Woodland subzones and the Namib subzone were treated as hypothetically valid zones, as indicated in Table 1. The list excludes feral and exotic species, as well as poorly known endemics of doubtful taxonomic status. As far as possible, the natural (historic) ranges of species were considered, thus compensating for human impact. Species with extremely limited ranges, or known from only a few localities, were considered as representative of the biotic zone in which they occur. Where the majority of localities for a species fall within a given zone, with only a few isolated instances falling just inside an adjacent zone, these were considered as typical only of the zone where the distribution is concentrated, and not as a constituent of the mammal fauna of the second zone. However, if such scattered localities are deep into the second zone, they were considered typical of that zonal fauna as well. Judgment was subjective. Typical Forest zone species occurring outside that zone, but restricted to riverine forests, were considered as pure forest zone species. However, the influence of dispersal corridors, such as the Kuiseb and Orange rivers, was not taken into account.

The distribution of bats as a group is particularly poorly documented, which may adversely influence the results of this analysis. Excluding bats was considered. However, certain mammalian taxa, as well as nutritionally and ecologically adapted groups, demonstrate diverse latitudinal clinal trends in composition and densities (Nel, 1975). Thus it was decided to include the meager information on bats in an effort to retain a more balanced image of trends in overall mammalian ecological distribution.

A simple matrix of similarity, indicating the degree of interrelationships of mammalian faunas of southern African biotic zones, is given in Table 2. Absolute numbers of species in common are indicated below the diagonal. Italic numerals on the diagonal indicate the number of species in each zone, and the bracketed numerals underneath these denote the known number of endemic species. Above the diagonal is an index of faunal resemblance, calculated after Duellman (1965).

Table 1.—*Distribution of southern African mammals according to Biotic Zones.*

	Biotic Zones					
Taxa	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
Petrodromus tetradactylus	—	—	—	X	—	X
Macroscelides proboscideus	X	X	—	—	—	—
Elephantulus intufi	X	X	—	X	—	—
Elephantulus rupestris	—	X	—	—	—	—
Elephantulus myurus	—	—	—	X	X	—
Elephantulus edwardi	—	X	—	—	—	—
Elephantulus brachyrhynchus	—	—	—	X	X	—
Erinaceus frontalis	—	X	—	X	X	—
Myosorex varius	—	—	X	X	X	X
Myosorex cafer	—	—	—	X	X	X
Suncus lixus	—	—	—	X	—	—
Suncus gracilis	—	—	—	—	X	—
Sylvisorex megalura	—	—	—	—	—	X
Crocidura occidentalis	—	—	—	X	—	X
Crocidura flavescens	—	—	X	—	X	X
Crocidura luna	—	—	—	—	—	X
Crocidura mariquensis	—	—	—	X	X	—
Crocidura hirta	—	X	—	X	X	X
Crocidura silacea	—	—	—	X	X	X
Crocidura cyanea	X	X	—	X	X	X
Crocidura maquassiensis	—	—	—	X	X	—
Crocidura bicolor	—	X	—	X	—	—
Chrysospalax trevelyani	—	—	—	X	—	X
Chrysospalax villosus	—	—	—	X	X	X
Cryptochloris wintoni	—	X	—	—	—	—
Cryptochloris zyli	—	—	X	—	—	—
Chrysochloris asiatica	—	X	—	—	—	—
Chrysochloris visagiei	—	X	—	—	—	—
Eremitalpa granti	X	X	X	—	—	—
Chlorotalpa sclateri	—	X	—	—	X	—
Chlorotalpa duthiae	—	—	—	—	—	X
Chlorotalpa arendsi	—	—	—	—	—	X
Galcochloris obtusirostris	—	—	—	X	—	—
Amblysomus gunningi	—	—	—	—	—	X
Amblysomus hottentotus	—	—	—	X	X	X
Amblysomus iris	—	—	—	X	X	X
Amblysomus julianae	—	—	—	X	X	—
Eidolon helvum	—	X	—	X	X	—
Epomophorus wahlbergi	—	—	—	X	—	X
Epomophorus gambianus	—	—	—	X	—	—
Epomophorus crypturus	—	—	—	X	—	—
Epomophorus angolensis	—	—	—	X	—	—
Rousettus aegyptiacus	—	—	—	X	—	X
Rousettus angolensis	—	—	—	—	—	X
Taphozous mauritianus	—	—	—	X	—	—
Taphozous perforatus	—	—	—	X	—	—
Coleura afra	—	—	—	X	—	—
Nycteris hispida	—	—	—	—	—	X
Nycteris grandis	—	—	—	—	—	X
Nycteris macrotis	—	—	—	X	—	X
Nycteris woodi	—	—	—	X	—	X
Nycteris thebaica	X	X	—	X	—	X
Rhinolophus hildebrandti	—	—	—	X	—	X
Rhinolophus fumigatus	—	X	—	X	—	—
Rhinolophus clivosus	—	—	X	X	X	X

Table 1.—*Continued.*

	Biotic Zones					
Taxa	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
Rhinolophus darlingi	X	X	—	X	—	—
Rhinolophus landeri	—	—	—	X	—	—
Rhinolophus blasii	—	—	—	X	—	—
Rhinolophus capensis	—	X	X	X	—	—
Rhinolophus simulator	—	—	—	X	—	—
Rhinolophus denti	—	X	—	X	—	—
Rhinolophus swinnyi	—	—	—	X	—	—
Hipposideros commersoni	—	X	—	X	—	—
Hipposideros caffer	—	X	—	X	—	X
Triaenops persicus	—	—	—	X	—	—
Cloeotis percivali	—	—	—	X	—	—
Myotis welwitschii	—	—	—	X	X	—
Myotis seabrai	—	X	—	—	—	—
Myotis lesueuri	—	—	X	—	—	—
Myotis tricolor	—	X	—	X	X	—
Myotis bocagei	—	—	—	X	—	—
Nycticeius schlieffeni	—	X	—	X	—	—
Pipistrellus nanus	—	—	—	X	—	X
Pipistrellus kuhli	—	—	—	X	—	X
Pipistrellus rusticus	—	—	—	X	—	X
Pipistrellus rueppelli	—	—	—	X	—	—
Eptesicus rendalli	—	—	—	X	—	—
Eptesicus hottentotus	X	X	—	X	—	—
Eptesicus melckorum	—	—	X	—	—	—
Eptesicus zuluensis	X	X	—	X	—	—
Eptesicus somalicus	—	—	—	X	—	—
Eptesicus capensis	—	X	—	X	X	—
Eptesicus notius	—	—	X	—	—	—
Glauconycterus variegata	—	—	—	X	—	—
Laephotis wintoni	—	—	—	X	—	—
Scotophilus gigas	—	—	—	X	—	—
Scotophilus nigrita	—	—	—	X	—	—
Scotophilus leucogaster	—	X	—	X	—	—
Kerivoula argentata	—	—	—	X	—	—
Kerivoula harrisoni	—	—	—	X	—	—
Kerivoula lanosa	—	—	—	X	—	X
Miniopterus fraterculus	—	—	—	X	—	—
Miniopterus schreibersi	X	X	—	X	X	X
Otomops martiensseni	—	—	—	X	—	—
Sauromys petrophilus	—	X	—	X	—	—
Tadarida acetabulosus	—	—	—	X	—	—
Tadarida midas	—	X	—	X	—	—
Tadarida niveiventer	—	—	—	X	—	—
Tadarida condylura	—	—	—	X	—	X
Tadarida nigeriae	—	X	—	X	—	—
Tadarida chapini	—	—	—	X	—	—
Tadarida pumila	—	—	—	X	—	—
Tadarida fulminans	—	—	—	X	—	—
Tadarida aegyptiaca	—	X	X	X	X	X
Tadarida ansorgei	—	—	—	X	—	—
Galago crassicaudatus	—	—	—	X	—	X
Galago senegalensis	—	X	—	X	—	X
Papio cynocephalus	—	—	—	X	—	—
Papio ursinus	X	X	X	X	X	X
Cercopithecus mitis	—	—	—	X	—	X

Table 1.—*Continued.*

	Biotic Zones					
Taxa	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
Cercopithecus aethiops	—	X	—	X	—	X
Manis temmincki	—	X	—	X	X	—
Otocyon megalotis	—	X	—	X	—	—
Vulpes chama	X	X	—	X	X	—
Canis mesomelas	X	X	—	X	X	—
Canis adustus	—	—	—	X	—	—
Lycaon pictus	—	X	—	X	—	—
Ictonyx striatus	X	X	—	X	—	—
Poecilogale albinucha	—	X	—	X	X	—
Mellivora capensis	—	X	—	X	—	—
Lutra maculicollis	—	X	—	X	X	—
Aonyx capensis	—	X	—	X	X	—
Nandinia binotata	—	—	—	—	—	X
Viverra civetta	—	—	—	X	—	—
Genetta genetta	X	X	X	X	X	—
Genetta tigrina	—	—	X	X	—	X
Genetta rubiginosa	—	—	—	X	—	—
Genetta mossambica	—	—	—	X	—	—
Suricata suricatta	X	X	—	—	X	—
Paracynictis selousi	—	—	—	X	—	—
Bdeogale crassicauda	—	—	—	X	—	—
Cynictis penicillata	—	X	—	X	X	—
Herpestes ichenumon	—	—	—	X	—	—
Herpestes pulverulentus	—	X	—	—	X	—
Herpestes sanquineus	—	X	—	X	X	X
Herpestes ratlamuchi	—	X	—	X	—	—
Rhynchogale melleri	—	—	—	X	—	X
Ichneumia albicauda	—	—	—	X	—	X
Atilax paludinosus	—	X	X	X	X	X
Mungos mungo	—	X	—	X	—	—
Helogale parvula	—	X	—	X	—	—
Proteles cristatus	X	X	—	X	X	—
Hyaena brunnea	X	X	—	X	X	—
Crocuta crocuta	X	X	—	X	X	—
Felis libyca	X	X	X	X	X	—
Felis nigripes	—	X	—	—	X	—
Felis serval	—	—	X	X	—	—
Felis caracal	X	X	—	X	X	—
Panthera pardus	X	X	X	X	X	X
Panthera leo	—	X	X	X	X	—
Acinonyx jubatus	—	X	—	X	—	—
Orycteropus afer	—	X	—	X	X	—
Loxodonta africana	—	X	—	X	—	—
Procavia capensis	X	X	X	X	X	X
Procavia welwitschii	X	X	—	—	—	—
Heterohyrax brucei	—	—	—	X	—	—
Dendrohyrax arboreus	—	—	—	X	—	—
Diceros bicornis	—	X	X	X	—	—
Ceratotherium simum	—	X	—	X	X	—
Equus zebra	X	X	—	—	—	—
Equus burchelli	—	X	X	X	X	—
Potamochoerus porcus	—	—	X	X	—	X
Phacochoerus aethiopicus	—	X	—	X	—	—
Hippopotamus amphibius	—	X	X	X	X	—
Giraffa camelopardalis	—	X	—	X	—	—

Table 1.—*Continued.*

	Biotic Zones					
Taxa	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
Cephalophus natalensis	—	—	—	X	—	X
Cephalophus monticola	—	—	—	X	—	X
Sylvicapra grimmia	—	X	X	X	X	—
Raphicerus campestris	—	X	X	X	X	—
Raphicerus melanotis	—	—	X	X	—	—
Raphicerus sharpei	—	—	—	X	—	—
Ourebia ourebi	—	—	—	X	X	—
Neotragus moschatus	—	—	—	X	—	—
Oreotragus oreotragus	X	X	—	X	—	—
Madoqua kirki	—	X	—	—	—	—
Pelea capreolus	—	X	X	X	X	—
Redunca arundinum	—	—	—	X	—	—
Redunca fulvorufula	—	—	—	X	X	—
Kobus ellipsiprymnus	—	X	—	X	—	—
Kobus vardoni	—	—	—	X	—	—
Kobus leche	—	—	—	X	—	—
Aepyceros melampus	—	X	—	X	—	—
Aepyceros petersi	—	X	—	X	—	—
Antidorcas marsupialis	X	X	—	—	X	—
Oryx gazella	X	X	—	X	—	—
Hippotragus leucophaeus	—	—	X	—	—	—
Hippotragus niger	—	—	—	X	—	—
Hippotragus equinus	—	—	—	X	—	—
Damaliscus lunatus	—	—	—	X	—	—
Damaliscus dorcas dorcas	—	—	X	—	—	—
Damaliscus dorcas phillipsi	—	X	—	—	X	—
Alcelaphus buselaphus	—	X	—	X	X	—
Alcelaphus lichtensteini	—	X	—	X	—	—
Connochaetes taurinus	—	X	—	X	—	—
Connochaetes gnou	—	—	—	—	X	—
Tragelaphus scriptus	—	—	X	X	—	—
Tragelaphus spekei	—	—	—	X	—	—
Tragelaphus angasi	—	—	—	X	—	—
Tragelaphus strepsiceros	—	X	—	X	—	—
Taurotragus oryx	—	X	X	X	X	—
Syncerus caffer	—	—	—	X	—	—
Lepus capensis	—	X	—	X	X	—
Lepus saxatilis	—	X	—	X	X	—
Bunolagus monticularis	—	X	—	—	—	—
Pronolagus crassicaudatus	—	—	—	X	—	—
Pronolagus rupestris	—	X	—	X	X	—
Pronolagus randensis	—	X	—	X	X	—
Bathyergus janetta	—	X	—	—	—	—
Bathyergus suillus	—	—	X	—	—	X
Georychus capensis	—	X	X	—	X	—
Cryptomys damarensis	—	X	—	—	—	—
Cryptomys hottentotus	—	X	—	X	X	X
Hystrix africaeaustralis	X	X	—	X	X	X
Petromus typicus	X	X	—	—	—	—
Thryonomys swinderianus	—	—	—	X	—	—
Thryonomys gregorianus	—	—	—	X	—	—
Xerus inauris	—	X	—	—	X	—
Xerus princeps	—	X	—	—	—	—
Heliosciurus rufobrachium	—	—	—	X	—	X
Funisciurus congicus	—	X	—	—	—	—

Table 1.—*Continued.*

	Biotic Zones					
Taxa	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
Paraxerus palliatus	—	—	—	—	—	X
Paraxerus cepapi	—	—	—	X	—	—
Pedetes capensis	X	X	—	X	X	—
Graphiurus ocularis	—	X	X	—	—	—
Graphiurus platyops	—	X	—	X	X	—
Graphiurus murinus	—	X	—	X	X	X
Cricetomys gambianus	—	—	—	X	—	X
Dendromus nyikae	—	—	—	—	—	X
Dendromus melanotis	—	X	X	X	X	X
Dendromus mesomelas	—	—	X	X	X	X
Dendromus mystacalis	—	—	—	X	X	X
Malacothrix typica	—	X	—	—	X	—
Mystromys albicaudatus	—	—	X	—	X	—
Petromyscus monticularis	—	X	—	—	—	—
Petromyscus collinus	X	X	—	—	—	—
Saccostomus campestris	—	X	X	X	X	—
Steatomys pratensis	—	X	—	X	—	—
Steatomys krebsi	—	X	—	—	X	—
Steatomys minutus	—	X	—	X	X	—
Acomys spinosissimus	—	—	—	X	—	X
Acomys subspinosus	—	—	X	—	—	X
Aethomys granti	—	X	—	—	—	—
Aethomys namaquensis	X	X	X	X	X	—
Aethomys chrysophilus	—	X	—	X	—	—
Aethomys nyikae	—	—	—	X	—	—
Dasymus incomtus	—	—	X	X	X	—
Mus indutus	—	—	—	X	X	—
Mus minutoides	X	X	X	X	X	X
Lemniscomys griselda	—	X	—	X	—	—
Pelomys fallax	—	—	—	X	—	X
Praomys natalensis	—	X	X	X	X	X
Praomys shortridgei	—	—	—	X	—	—
Praomys verreauxi	—	—	X	—	—	X
Rhabdomys pumilio	X	X	X	X	X	X
Thallomys paedulcus	X	X	—	X	—	—
Thamnomys cometes	—	—	—	—	—	X
Thamnomys dolichurus	—	—	—	X	—	X
Zelotomys woosnami	—	X	—	—	—	—
Parotomys brantsi	X	X	X	—	—	—
Parotomys littledalei	X	X	—	—	—	—
Otomys laminatus	—	—	—	X	X	X
Otomys angoniensis	—	X	—	X	X	—
Otomys saundersiae	—	—	X	—	X	—
Otomys irroratus	—	X	X	X	X	X
Otomys sloggetti	—	—	—	—	X	—
Otomys unisulcatus	—	X	—	—	—	—
Desmodillus auricularis	X	X	—	—	—	—
Gerbillurus vallinus	X	X	—	X	—	—
Gerbillurus tytonis	X	—	—	—	—	—
Gerbillurus paeba	X	X	X	X	—	—
Gerbillurus setzeri	X	—	—	—	—	—
Tatera leucogaster	X	X	—	X	—	—
Tatera afra	—	—	X	—	—	—
Tatera brantsii	—	X	—	X	X	—
Tatera inclusa	—	—	—	X	—	—

Table 1.—*Continued.*

Taxa	Namib	South West Arid	South West Cape	Southern Savanna Woodland	Southern Savanna Grassland	Forest
	Biotic Zones					
Total (275 species)	43	136	50	209	91	73
Percentage of total fauna	15.6	49.5	18.2	76.0	33.1	26.6
Total no. of endemic species	2	16	7	60	3	12
Percentage endemics to total zonal fauna	4.65	11.76	14.00	28.71	3.30	16.44

DISCUSSIONS

It must be stressed that subcontinental distributional data is as yet incomplete for the majority of species, particularly so in the Cape Province and South West Africa. Furthermore, the accuracy of this analysis will be greatly enhanced if conducted on the subspecies level, rather than on a species level. This ideal will be delayed for many years as a result of the unsatisfactory status of the knowledge of subspeciation in southern African mammals.

On the other hand, a more intimate knowledge of the distribution patterns of species does not necessarily imply a high incidence of range extensions into biotic zones where they have previously been unrecorded. When species' geographic ranges are better known and the occurrence of not too many species are recorded in new zones, the results of this analysis will not change dramatically. A more accurate FRF analysis facilitated by subspecies consideration will probably only enhance the findings of this treatment because a higher degree of endemism is expected. Whatever the case, the following points are pertinent from Table 2 and warrant further comment here, especially with regard to my aim to assess the validity of biotic zones as viable biogeographical areas.

Superficially, the FRF indices of all zones under consideration are low enough to warrant their consideration as distinct zones (Table 2). Closer scrutiny is however essential.

The Namib is most closely related to the South West Arid, albeit with a FRF index as low as 0.458. The Namib's FRF indices when calculated against the other zones are, however, much lower, which confirms distinctness from these. The Namib possesses only two endemic species (Table 1), namely *G. tytonis* and *G. setzeri*. However, by far the greatest majority (41) of the Namib's total mammal fauna (43) consists of a faction of the bigger South West Arid fauna (some species also occur elsewhere).

Table 2.—*Resemblance of mammalian faunas of the six southern African Biotic Zones and Subzones. (See text for explanation; italic numerals on diagonal indicate total number of species in zone, the numerals in brackets underneath these denote the known number of endemic species).*

Biotic Zones	Southern Savanna Woodland	South West Arid	Southern Savanna Grassland	Forest	South West Cape	Namib
Southern Savanna Woodland	*209* (60)	.580	.500	.404	.247	.238
South West Arid	100	*136* (16)	.573	.201	.290	.458
Southern Savanna Grassland	75	65	*91* (3)	.341	.411	.299
Forest	57	21	28	*73* (12)	.309	.138
South West Cape	32	27	29	19	*50* (7)	.237
Namib	30	41	20	8	11	*43* (2)

Consequently it can be considered as merely a depauperate fauna of the latter, resulting from the inhospitable nature of the Namib. The Namib's biogeographical uniqueness thus lies not so much in its typical endemic fauna, or its faunal composition for that matter, but rather in the fauna it does not possess. The Namib is therefore considered here as a biotic zone of full rank. Detailed analysis has shown that the Namib can be further subdivided, on the basis of the sand dunes being faunistically more depauperate than the gravel plains (see Coetzee, 1969).

In spite of its tremendous floral diversity, the South Western Cape is also very depauperate in mammalian fauna. However, it must be pointed out that this is, in terms of intensive mammal surveying, the most neglected biotic zone of all. It has seven endemic taxa as far as is known—*C. zyli, M. leseuri, E. melckorum, E. notius, D. d. dorcas, T. afra*, and the extinct *H. leucophaeus* (see Table 1). The remainder of the faunal element is made up of mammalian species shared with other biotic zones. This zone shares 32 species with the Woodland zone, and 29 with the Grassland zone. However, as a result of the enormous differential species diversity between the Woodland and the South West Cape, the FRF analysis indicates a closer resemblance between the latter zone and the less diversified Grassland zone, with an index of 0.411. It is interesting to note that the South West Cape and the Grassland zones are unconnected.

The Forest zone is also quite distinct from the others. It is faunistically most closely related to the Southern Savanna Woodland subzone with a FRF index of 0.401. It possesses 12 endemic species (see Table 1).

The Woodland and Grassland zones and the South West Arid zone are the three areas related more closely to each other than any other combination of zones. Their individual FRF indices in relation to each other are however considered low enough to warrant their individual recognition. Because the Grassland has been considered a subzone of the Southern Savanna biotic zone, closest resemblance is expected between it and the related Woodland subzone. This is, however, not the case. Both in terms of absolute number of species in common and FRF index, the Woodland and South West Arid are faunistically most closely related (100 species in common; FRF index 0.580). This is followed by a closer resemblance between Grassland and South West Arid in terms of FRF indices (0.573), but in terms of number of species in common, a closer resemblance between Grassland and Woodland (75 species). This inconsistency can be ascribed to the disproportionate sizes of the three zonal faunas and as compensated for by Duellman's formula, especially designed for such instances. The Southern Savanna Woodland has by far the richest mammalian fauna; 209 species, representing 76.0% of the total southern African mammalian fauna, occur here, including 60 endemics (predominantly bats). This is followed by the South West Arid, with a total diversity of 136 species, that is 49.5% of the total of 275 southern African species, with 16 endemics. The Savanna Woodland undoubtedly offers the highest variety of habitats, being ecologically more diversified both horizontally and vertically. Its rich species diversity could be related to this fact more than any other.

The temptation is great to assume that the respective faunal elements of other zones have originated by a radiation of Woodland-adapted species. Undoubtedly this is true in many instances, especially in the case of species, which do not rely on trees as an integral element in their habitat requirements. On the other hand, the high number of endemics typical of the Woodland and South West Arid areas combined (76 species) can be interpreted as a faunal element specialized towards a dependence on woodland in some manner or other. The fact that such a large portion (100 species) of the non-endemic fauna of the Woodland apparently radiated adaptively into the South West Arid is reflected by the highest FRF index of all (0.580). Mostly due to lower average annual precipitation, the latter zone has a less developed woodland flora, and consequently a less diversified mammalian fauna.

The same situation could also be demonstrated with Grassland-adapted species finding suitable habitat in adjacent Woodland Savanna (FRF index 0.500) and South West Arid (FRF index 0.573). Forest is scattered through three zones (Southern Savanna Woodland, Southern Savanna Grassland, and South West Cape), and has higher FRF indices with these than with the non-adjacent Namib and South West Arid. This trend of a relatively higher FRF index reflecting a sharing of species between adjacent zones, numerically radiating clinally from the Woodland Savanna, appears to be the rule. There is one exception, that is South West Cape being faunistically closest to the non-adjacent Grassland, with a FRF index of 0.423.

Nel (1975) found an almost linear correlation between number of species and mean annual precipitation in a latitudinal direction in southern Africa. The result is a low-to-high gradient in species densities from west to east, as mean annual rainfall increases. This is particularly the case with bats. Nel could also find no real correlation between species density and altitude. The altitudinal profile of southern Africa is relatively low, which probably explains this phenomenon. This, however, needs closer study to confirm its validity.

It would appear from the results of this analysis that a low-to-high gradient in species densities could also be demonstrated in a south to north direction. Species densities increase from 50 in the South West Cape, to 91 in the Grassland, to 136 in the South West Arid, to 209 in the Woodland. Although rainfall again undoubtedly plays some role in this trend, other causal factors such as decreasing latitude, temperature, faunal origin, and dispersion, will have to be considered in a more detailed analysis.

CONCLUSIONS

1) Six biotic zones are recognized as viable biogeographical entities, as deduced from this analysis. Where the Grassland and the Woodland have formerly been regarded as subzones of the then Southern Savanna biotic zone, terminology may hence be confusing when referring to these as biotic zones of full rank. In order to retain the Pan-African implications and perspective of the term Southern Savanna, I suggest that these two biotic zones be known as the Southern Savanna Woodland and the Southern Savanna Grassland biotic zones. This suggestion is made in the full realization that in the latter case, the definition of a savanna is stretched to the limit. Terminology for the Namib biotic zone remains unchanged, indicating its elevated zonal status.

2) Biotic zones are here regarded as the largest biogeographic units in which southern Africa could be subdivided, that is Southern Savanna Woodland, Southern Savanna Grassland, Forest, Namib, South West Arid, and South West Cape.

3) Very few species have such a wide habitat tolerance that they occur in all biotic zones. Endemism is, on the other hand, equally as unusual. In the majority of instances, species are shared between various combinations of zones, and the unique feature of the FRF analysis is to take this into account, apart from endemism. Therefore, a high FRF index indicates a high incidence of shared species and therefore closer faunal similarity.

4) The FRF analysis in fact takes three characteristics into consideration when expressing the faunal distinctness of a zone: the respective species densities of the two zones under consideration; the number of species in common; and indirectly the number of distinctive species of each zone. Based on the results of the FRF analysis, the Namib zone is deduced to be fully distinct from the South West Arid. It is considered a bona fide biotic zone in full realization of the fact that it has a very small distinctive fauna. The Grassland is similarly considered to be a distinct biotic zone, rather than a subzone. In both these instances, one of the previous considerations for their recognition as zones of lower rank was the low degree of endemism.

5) The six biotic zones recognized here as biogeographical entities, correlate very well with what I regard as major ecological biomes in southern Africa.

6) The FRF indices of the South West Arid, the Woodland, and the Grassland, as compared with each other, are all over 0.500. There is no established value over which a zone cannot be considered statistically valid, and judgment is therefore subjective. The FRF value of these zones in question is here considered low enough to warrant their recognition as valid biotic zones. In comparison Armstrong (1972) considers Merriam's (1890) life zones, which the former author tested with Duellman's FRF analysis, as valid with indices as high as 0.847. In the present analysis, the generally lower FRF indices could also be ascribed to disproportionate faunal densities between certain zones. These differences between the sizes of zonal faunas are here regarded as valid criteria in considering the rank of a particular zone.

7) With the exception of seven species, the remainder of the 68 southern African bat species are all recorded from the Southern Savanna Woodland, among other zones. The presence of the bat fauna in the other biotic zones is dramatically less (five in the Namib; 20 in the South West Arid; six in the South West Cape; seven in the Grassland; and 18 in the Forest). The Chiroptera is the least known group of mammals in southern Africa, and although Duellman's (1965) formula partly compensates for

this shortcoming, it has an undetermined bearing on the accuracy of the above observation. The inference is, however, that as a group bats have a remarkable attachment to Woodland Savanna.

8) Biotic zones are empirically derived by consideration of major vegetation types. Although the former are proved to be significant from a faunal point of view, it does not necessarily reflect the best way to describe faunal distribution patterns, especially because individual geographic ranges of species seldom overlap entirely with any biotic zone. Biotic zones as significant biogeographical entities should rather, from a faunal point of view, be seen as illustrating the gross direct relationship of the animal to its floral environment, and to a lesser extent, to the physical environment. In the context of biotic zones, faunal interrelationships should therefore be interpreted from an ecological point of view.

9) Continued intensive mammal surveying in southern Africa is considered essential for a better understanding of both subspeciation and zoogeographical interpretation, through more detailed analysis. Especially the Chiroptera throughout the subcontinent, and the faunas of South West Arid and South West Cape biotic zones, need intensive attention in terms of surveying. It is, however, not expected that a more intimate knowledge of these aspects will dramatically change the results and implications of this analysis.

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This paper is introductory to a detailed zoogeographical analysis of distribution patterns of Transvaal mammals. It is aimed at establishing the credibility of biotic zones as major biogeographical entities within this Province in order to facilitate further subdivision into community-types. The research on the distribution of Transvaal mammals has been jointly sponsored by the Transvaal Museum and the South African Council for Scientific and Industrial Research, to whom I express my gratitude.

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KARYOTYPIC DATA FOR AFRICAN MAMMALS, WITH A DESCRIPTION OF AN *IN VIVO* BONE MARROW TECHNIQUE

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ABSTRACT

Basic information, which should be included in any publication on the chromosomes of mammals, is given. A field-tested bone marrow-*in vivo* method of karyotyping is presented. A review of the literature concerning karyotypes of African mammals was done and these karyotypic data are listed for 292 species and subspecies of African mammals.

INTRODUCTION

Karyotypes have proven to be valuable data for evolutionary and systematic studies. A summary of chromosomal data for African mammals is presented in Appendix I. For maximum value, any publication on the chromosomes of a species should contain the following information:

1. A photomicrograph of the karyotype. This is necessary if this is the first report for a species or if your karyotypic data differs from that previously published for the species.
2. Diploid Number.
3. "Nombre fundamental" or number of arms of the autosomal complement.
4. Morphology of sex chromosomes.
5. Sex of specimens examined.
6. Number of specimens examined.
7. Geographic origin of specimen examined.
8. Museum where voucher specimens are deposited (with museum numbers, if possible).
9. Minimum number of spreads examined from any specimen included.

METHODS AND TECHNIQUES

Preparation of somatic chromosomes is a simple process which can be conducted in the field. For the bone marrow-*in vivo* technique described below, live animals are required. The following technique is modified after Baker (1970).

1. Inject the live animal intraperitoneally with a 0.03% Vinblastine (Velban of Eli Lilly & Co.) or colchicine solution at 0.01 ml per gram of body weight.

2. After two hours sacrifice the animal and remove a long bone, such as the femur in rodents or the humerus in bats, without damaging the proximal end. Remove the flesh and a chip of bone from the proximal end to expose the red bone marrow cavity. Flush the shaft with 3 ml of a 1.0% sodium citrate solution. Pipette vigorously to break up any cell clumps. The sodium citrate solution will support bacterial growth and should be prepared daily under field conditions.

3. Let the resultant cell-suspension set for about 10 min.

4. Centrifuge the suspension at 1,500 RPM for 4 min.

5. Discard as much of the supernatant fluid as possible, being careful to leave the button of cells undisturbed. Add 3 ml of freshly prepared Carnoy's fixative (3 parts absolute methanol:1 part glacial acetic acid). Floating material and lipids may be removed at this stage. Disrupt the cell button with a pipette until the cell suspension is homogeneous. Allow cells to fix for about 10 min.

6. Centrifuge for 4 min and decant supernate. Resuspend cells in 1.0 ml of fixative and centrifuge as before. This step is repeated at least three times. After final washing, cells are resuspended in 1.0 ml of fixative.

7. Place two or three drops of cell suspension on a clean slide and ignite. When the fire extinguishes itself, the residue is promptly slung from the slide. Four slides from each specimen are usually made.

8. Dry slides are stained for 12 min in a 2% Giemsa stain (1 ml of Giemsa's stock solution in 50 ml

of buffer). Buffer is made by mixing 0.469 g of NaH_2PO_4 and 0.937 g of Na_2HPO_4 in 1,000 ml of distilled water. The buffered stain can be used to stain three or four sets of slides. If the buffer solution is unavailable, then staining can be by other methods such as one part Giemsa's stock solution to eight parts distilled water for 15 min. If staining with the latter solution is poor, heating the stain to near 50°C will often help. This distilled water base stain can be used to stain only one set of slides and then new stain must be mixed.

9. When a slide is removed from the stain it must be quickly rinsed with distilled water or a film of stain will cover the slide. Slide should be dry before covering with balsam or permount and a 22 by 40 mm coverslip.

Voucher specimens, with accurate collection data, should be deposited in a reputable museum. The tag on the voucher specimen should show that this specimen was karyotyped and microscope slides should be cross referenced to the voucher specimen.

TERMINOLOGY

Metacentric is a biarmed element that has arms of equal length (ratio is not greater than 1:1.1). Submetacentric is a biarmed element that has an arm ratio greater than 1:1.1 but less than 1:2. Subtelocentric is a biarmed element that has an arm ratio greater than 1:2, but a second short arm is clearly visible. Acrocentric (=telocentric for practical purposes) is an element that appears to be uniarmed when viewed with a light microscope. When calculating the nombre fundamental or number of arms of the autosomal complement, each metacentric, submetacentric, or subtelocentric is given a value of 2, whereas each acrocentric is given a value of 1. The nombre fundamental (NF) of Matthey includes the arms of the sex elements and auto, whereas the "number of arms of the autosomal complement" (AA Appendix I) does not include the sex elements.

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Appendix I.—Chromosomal data for African mammals. Orders are listed in classical phylogenetic arrangement. Families, genera, and species are in alphabetical order. 2N = diploid number; NF = Nombre Fundamental, which includes sex elements; AA = number of arms of autosomal complements; BA = number of biarmed autosomes. M, SM, ST, and A are defined in text.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Insectivora								
Erinaceidae								
Erinaceus algirus	48	—	—	—	—	—	—	Gropp and Natarajan, 1972
Hemiechinus auritus aegyptius	48	—	—	—	X:M Y:small A	—	—	Gropp et al., 1969*b*
	48	—	92	46	X:M Y:small A	4	Egypt	de Hondt, 1974
Macroscelidae								
Elephantulus rufescens	34	—	—	—	—	—	—	Chu and Bender, 1962
Elephantulus rupestris jamesoni	30	—	—	—	—	—	—	Ford and Hamerton, 1956
Elephantulus rozeti	28	—	—	—	—	—	—	Matthey, 1954*a*
Nasilio b. brachyrhynchus	26	—	—	—	—	—	—	Stimson and Goodman, 1966
Soricidae								
Crocidura bottegi eburnea	40	—	—	—	—	—	Ivory Coast	Meylan, 1971
Crocidura jouvenetae ebriensis	44	—	—	—	—	—	Ivory Coast	Meylan, 1971
Crocidura occidentalis kiwu	50	—	—	—	X:large ST Y:small A	—	—	Meylan, 1967
Crocidura olivieri	50	—	56	8	X:SM Y:small A	4	Egypt	de Hondt, 1974
Crocidura poensis pamela	52	—	—	—	—	—	Ivory Coast	Meylan, 1971
Crocidura russula pulchra	42	—	—	—	—	—	Ivory Coast	Meylan, 1971
Crocidura suaveolens	40	—	—	—	—	—	—	Meylan, 1966
Crocidura theresae	50	—	—	—	—	—	Ivory Coast	Meylan, 1971
Sylvisorex megalura	48	96	—	46	—	1♂	Ivory Coast	Meylan, 1975
Tenrecidae								
Micropotamogale lamottei	38	76	—	—	—	—	Ivory Coast	Vogel et al., 1977
Chiroptera								
Molossidae								
Otomops martiensseni	48	—	56	—	X:SM; Y:A	1	—	Dulić and Mutere, 1973
Platymops setiger	48	—	54	—	X&Y:SM	1	—	Warner et al., 1974
Tadarida bivittata	48	—	54	8	X:M; Y:A	4	Kenya, Rhodesia	Peterson and Nagorsen, 1975
Tadarida condylura	48	—	56	—	X:SM; Y:A	6	—	Dulić and Mutere, 1973

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Tadarida fulminans	48	—	54	8	X:SM; Y:A	4	Rhodesia	Peterson and Nagorsen, 1975
Tadarida pumila	48	—	58	—	X:SM; Y:SM	9	—	Dulić and Mutere, 1973
Nycteridae								
Nycteris thebaica	42	—	78	38	X:SM; Y:small M	6	Rhodesia	Peterson and Nagorsen, 1975
Pteropidae								
Eidolon helvum	34	—	—	—	—	—	—	Matthey, 1962
Epomophorus anurus	36	72	—	—	—	1♀	—	Dulić and Mutere, 1973*b*
Epomophorus crypturus	35 (♂) 36 (♀)	—	68	34	—	1♂, 1♀	Rhodesia	Peterson and Nagorsen, 1975
Epomophorus gambianus	35	—	68	34	X:SM	2♀♀	Rhodesia	Peterson and Nagorsen, 1975
Epomophorus wahlbergi	36	72	—	—	X:SM; Y:A	1♂	—	Dulić and Mutere, 1973*b* Dulić and Mutere, 1977
	36	—	68	34	—	2♀♀	Rhodesia	Peterson and Nagorsen, 1975
Epomops franqueti	36	—	68	34	—	2♀♀	Kenya	Peterson and Nagorsen, 1975
Rousettus aegyptiacus leachi	36	—	66	—	X:SM; Y:minute	—	—	Dulić and Mutere, 1973*b* Dulić and Mutere, 1977
Rhinolophidae								
Aselia tridens	50	—	62	14	X:ST; Y:A	9	Tunisia	Baker et al., 1975
Hipposideros caffer	32	—	60	30	X:ST; Y:A	2	Rhodesia	Peterson and Nagorsen, 1975
	32	—	60	30	X:M	1	Kenya	Dulić and Mutere, 1973*b*
Rhinolophus clivosus	58	—	62	6	X:large A; Y:small A	4	—	Dulić and Mutere, 1974
Rhinolophus darlingi	50	—	60	4	X&Y:ST	2	Rhodesia	Peterson and Nagorsen, 1975
Rhinolophus denti	58	—	62	6	X:ST	2	Rhodesia	Peterson and Nagorsen, 1975
Rhinolophus euryale	58	—	60	—	—	—	Europe	Bovey, 1949 Manfreddi Romanini et al., 1975
Rhinolophus ferrumequinum	58	—	60	4	X:SM; Y:A	2♂♂	Tunisia	Baker et al., 1975

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Rhinolophus hildebranti	58	—	60	4	X&Y:ST	5	Rhodesia	Peterson & Nagorsen, 1975
Rhinolophus hipposideros	56	—	60	—	—	—	Europe	Capanna et al., 1967
Rhinolophus mehelyi	58	—	60	4	S:SM; Y:A	14	Tunisia	Baker et al., 1975
Triaenops afer	36	—	60	26	X:M; Y:small ST	3♂	—	Dulic and Mutere, 1977
Rhinopomatidae								
Rhinopoma hardwickii	36	—	—	—	—	—	—	Ray-Chandhuri and Pathak, 1966
Vespertilionidae								
Barbastella barbastellus	32	—	—	—	—	—	—	Bovey, 1949
	32	—	50	—	—	3♀♀	Europe	Manfreddi Romanini et al., 1975
Eptesicus capensis	32	—	50	20	X:SM; Y:A	3	Rhodesia	Peterson and Nagorsen, 1975
Eptesicus hottentotus	50	—	58	0	X:SM	2	Rhodesia	Peterson and Nagorsen, 1975
Eptesicus serotinus	50	—	48	—	X:SM	5	Tunisia	Baker et al., 1975
Miniopteris schreibersi	46	—	50	6	X:SM; Y:A	6 6	Europe Tunisia	Manfreddi Romanini et al., 1975 Baker et al., 1975
Myotis blythi	44	—	50	8	X:SM; Y:A	36	Tunisia	Baker et al., 1975
Myotis capaccinii	44	—	50	—	—	—	Europe	Manfreddi Romanini et al., 1975
Myotis myotis	44	—	50	—	—	—	Europe	Manfreddi Romanini et al., 1975
Pipistrellus kuhli	44	—	50	8	X:SM; Y:A	9	Tunisia	Baker et al., 1975
Pipistrellus nanus	36	—	50	16	X:M; Y:A	1♂	Rhodesia	Peterson and Nagorsen, 1975
Plecotus austriacus	32	—	50	20	X:M; Y:A	16	Tunisia	Baker et al., 1975
Scotophilus nigrita = *S. dinganii* (see Robbins, 1978)	36	—	—	—	—	1♀	Rhodesia	Peterson and Nagorsen, 1975
Primates								
Lorisidae								
Arctocebus calabarensis	52	102	—	—	X:SM	—	—	Egozcue and Egozcue, 1966 Chiarelli, 1974
Galago alleni	40	—	—	—	—	—	—	de Boer, 1972*a*
Galago crassicaudatus	62	variable	—	—	X:SM; Y:SM or A	—	—	Chu and Bender, 1961 Chiarelli, 1974

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Galago demidovii	58	—	—	—	—	—	—	de Boer, 1972*b*
Galago senegalensis	36–38	variable	—	—	X:SM; Y:SM or A	—	—	Matthey, 1955 Egozcue, 1970
Perodicticus potto	62	87	—	—	X:SM; Y:A	—	—	Chu and Bender, 1961 Chiarelli, 1974
Cercopithecidae								
Allenopithecus nigroviridis	60	—	—	—	—	—	—	Chiarelli, 1966
	48	—	92	46	X:SM; Y:small A	—	—	Hsu and Benirschke, 6(299), 1971
Cercocebus aterrimus	42	—	—	—	—	—	—	Chiarelli, 1962
Cercocebus galeritus	42	—	—	—	—	—	—	Chu and Bender, 1961
Cercocebus torquatus	42	—	80	40	X:SM; Y:M	—	—	Chu and Giles, 1957 Hsu and Benirschke, 5(246), 1971
Cercopithecus aethiops sabaceus	60	—	116	58	X:large SM; Y:small SM	—	—	Chu and Giles, 1957 Hsu and Benirschke, 1(48), 1967
Cercopithecus ascanius	66	—	112	48	X:SM; Y:small A	—	—	Wurster and Benirschke, 1969 Hsu and Benirschke, 6(300), 1971
Cercopithecus cephus	66	—	108	44	X&Y:SM	—	—	Chiarelli, 1963 Hsu and Benirschke, 5(247), 1971
Cercopithecus diana	60	—	—	—	—	—	—	Chu and Giles, 1957
Cercopithecus diana roloway	58	—	—	—	—	—	—	Chiarelli, 1962b
Cercopithecus hamlyni	64	—	—	—	—	—	—	de Boer, 1970
Cercopithecus lhoesti	72	—	—	—	—	—	—	Chu and Bender, 1961
Cercopithecus mitis	72	—	—	—	—	—	—	Bender and Chu, 1963
Cercopithecus mona campbelli	66	—	—	—	—	—	—	Chu and Giles, 1957
Cercopithecus mona denti	66	—	—	—	—	—	—	Tappen, 1960
Cercopithecus mona mona	66	—	—	—	—	—	—	Bender and Mettler, 1958
Cercopithecus mona preussi	66	—	—	—	—	—	—	Chiarelli, 1962
Cercopithecus nictitans	70	—	—	—	—	—	—	Kuhn, 1967

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Cercopithecus petaurista buttikoferi	66	—	—	—	—	—	—	Chu and Giles, 1957
Colobus badius	44	—	—	—	—	—	—	Kuhn, 1967
Colobus polycomos	44	—	—	—	—	—	—	Chiarelli, 1962
Erythrocebus patas	54	—	—	—	—	—	—	Chu and Giles, 1957
Miopithecus talapoin	54	—	86	38	X:SM; Y:small SM	—	—	Chiarelli, 1962 Hsu and Benirschke, 5(248), 1971
Papio sp. (*anubis*?)	42	—	80	40	X:SM; Y:small A	—	—	Darlington and Hague, 1955 Hsu and Benirschke, 5(248), 1971
Papio cynocephalus	42	—	—	—	—	—	—	Chiarelli, 1962
Papio gelada	42	—	—	—	—	—	—	Chiarelli, 1962
Papio hamadryas	42	—	—	—	—	—	—	Chiarelli, 1962
Papio leucophaeus	42	—	—	—	—	—	—	Chiarelli, 1962
Papio papio	42	—	—	—	—	—	—	Darlington and Hague, 1955
Papio ursinus	42	—	—	—	—	—	—	Ismail and Tobias, 1956
Pongidae								
Gorilla gorilla	48	—	78	32	X:large SM, Y:small SM	—	—	Hamerton et al., 1961 Hsu and Benirschke, 5(150), 1969
Gorilla gorilla beringei								Hamerton et al., 1963
Pan troglodytes	48	—	80	34	X:SM; Y:small A	—	—	Young et al., 1960 Chiarelli, 1962 Hsu and Benirschke, 3(148), 1969
Pan troglodytes paniscus	48	—	—	—	—	—	—	Chiarelli, 1961
Lagomorpha								
Leporidae								
Lepus capensis tolai	48	—	—	—	—	—	—	Vorontsov and Ivanitskaia, 1969
Oryctolagus cuniculus	44	72	—	—	X:SM; Y:SM	—	—	Melander, 1956 Hsu and Benirschke, 1(8), 1967

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Rodentia								
Bathyurigidae								
Georychus capensis	54	—	—	—	—	—	—	Matthey, 1956
Muridae								
Cricetinae								
Mystromys albicaudatus	32	—	—	—	—	—	South Africa	Matthey, 1954*c*
	32	—	60	30	X&Y:A	—	—	Hsu and Benirschke, 2(60), 1958
Dendromurinae								
Dendromus insignis kivu	48	—	—	—	—	—	—	Matthey, 1967
Dendromus melanotis	36	—	—	—	—	—	—	Matthey, 1970
Dendromus mystacalis messorius	38	—	—	—	—	—	—	Matthey, 1970
Malacothrix typica	38	—	—	—	—	—	—	Allenbach, 1964
Saccostomus campestris	46	—	—	—	X:SM	—	South Africa	Matthey, 1958
	44	—	—	—	—	—	—	Ford and Hamerton, 1956
Saccostomus mearnsi	40–42	—	—	—	—	4	Ethiopia	Hubert, 1978*a*
Steatomys pratensis	68	70	—	—	X:M; Y:SM	—	South Africa	Matthey, 1954*c*
Gerbillinae								
Desmodillus aricularis	52	70	—	—	X&Y:M	—	South Africa	Matthey, 1954*c*
Gerbillurus paeba	36	—	—	—	—	—	—	Matthey, 1958
Gerbillus allenbyi	40	80	—	—	—	—	—	Wahrman and Zahavi, 1955
Gerbillus amoenus	52	61, 62	—	—	—	—	Egypt	Wassiff et al., 1969
Gerbillus andersoni	40	80	—	38	—	—	Egypt	Wassiff et al., 1969
	40	—	76	—	—	—	Tunisia	Cockrum et al., 1977
Gerbillus aureus	74	—	92–100	20–28	X:SM; Y:A?	—	Tunisia	Jordan et al., 1975
Gerbillus calurus (=*Sekeetamys calurus*)	38	74	—	—	—	—	Egypt	Wahrman and Zahavi, 1955
								Wassiff et al., 1969
Gerbillus campestris	56	—	—	—	—	—	—	Matthey, 1953
	56	69–71	—	—	—	—	Egypt	Wassiff et al., 1969
	56	—	68	7	X&Y:SM	—	Tunisia	Jordan et al., 1975
Gerbillus dasyurus	60	66–68	—	—	—	—	Israel and N. Africa	Wahrman and Zahavi, 1955
	60	69–70	—	—	—	—	Egypt	Wassiff et al., 1969
Gerbillus garamantis	54	—	—	—	—	—	—	Matthey, 1954*c*
Gerbillus gerbillus	43 (♂)	79–81	—	—	—	—	—	Matthey, 1954*d*
	42 (♀)						Egypt	Wassiff et al., 1969
	43 (♂) 42 (♀)	—	74	18	X:ST; YY (♂):M?	—	Tunisia	Jordan et al., 1975

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Gerbillus henleyi	52	63–65	—	—	—	—	Egypt	Wassiff et al., 1969
Gerbillus nanus	52	66–68	—	—	—	—	—	Wahrman and Zahavi, 1955
	52	—	—	—	—	—	Egypt	Wassiff et al., 1969
	52	—	58	4	X:M; Y:A	9	Tunisia	Jordan et al., 1975
Gerbillus nigeriae	62–68	92–102	—	—	X:large A	—	Niger	Tranier, 1976*a*
Gerbillus perpallidus	40	—	—	—	—	—	—	Lay, 1975
Gerbillus pulvinatus	62	84	—	—	—	14	Ethiopia	Hubert, 1978*b*
Gerbillus pyramidum	40	80	74	18	—	—	Algeria	Matthey, 1952
	38	76	72	—	—	—	Egypt	Wassiff et al., 1969
	40	—	—	—	X&Y:M	—	Tunisia	Jordan et al., 1975
	40	78	—	—	—	1	Senegal	Hubert and Bohme, 1978
Gerbillus simoni	60	68–69	—	—	—	—	Egypt	Wassiff et al., 1969
(*kaiseri*)	60	—	—	8–10	—	—	Tunisia	Cockrum et al., 1976
Gerbillus tarabuli	40	—	—	—	—	—	—	Lay, 1975
Meriones crassus	60	60	—	—	—	—	—	Matthey, 1953
	60	74	—	—	—	—	—	Nadler and Lay, 1967
Meriones libycus	44	80–82	—	—	—	—	—	Matthey, 1953
	44	74	—	—	—	—	—	Nadler and Lay, 1967
	44	—	72	30	X:A; Y:SM	—	—	Hsu and Benirschke, 5(226), 1971
Meriones shawi	44	74	—	—	—	—	—	Matthey, 1957
	44	—	72	30	X&Y:SM	—	—	Hsu and Benirschke, 5(227), 1971
Pachyuromys duprasi	54	—	—	—	—	—	—	Matthey, 1954*e*
Psammomys obesus	48	—	—	—	—	—	—	Matthey, 1954*e*
	48	—	74	28	X:large SM; Y:small M	—	—	Hsu and Benirschke, 4(170), 1970
Tatera afra	44	70–76	—	—	—	—	South Africa	Matthey, 1954*c*
Tatera brantsi draco	44	70–76	—	—	X&Y:M	—	South Africa	Matthey, 1954*c*
Tatera gambiana	52	—	—	—	—	—	Senegal	Hubert et al., 1973
Tatera guineae	50	—	—	—	—	—	—	Matthey and Petter, 1970
Tatera hopkinsoni	48	—	—	—	—	—	Upper Volta	Matthey and Petter, 1970
Tatera kempi	36	—	—	—	—	—	C.A.E.	Matthey and Petter, 1970
Tatera nigrita	48	66, 70	—	—	—	—	Chad	Tranier, 1974
Tatera robusta	46	—	—	—	—	—	—	Matthey and Petter, 1970
Tatera schinzi	42	70–76	—	—	X&Y:M	—	—	Matthey, 1954*c*
Tatera valida	52	—	—	—	—	—	—	Matthey, 1969
*Taterillus arenarius** *(specimen = *T. nigeriae* of Matthey, 1969)	30	—	36	—	X:large M; Y:?	1♀	Mauritania	Robbins, 1974

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Taterillus congicus	54	68	—	—	—	—	C.A.E.	Matthey and Petter, 1970
	54	70	66	14	—	—	Chad	Tranier et al., 1974
	54	—	64	—	X:large SM; Y:small SM	—	C.A.E.	Genest and Petter, 1970 Robbins, 1977
Taterillus gracilis	23 (♂) 22 (♀)	—	—	—	—	—	Senegal	Matthey, 1969
	37 (♂) 36 (♀)	46, 48	—	—	X:M; Y:SM	—	Upper Volta	Matthey and Jotterand, 1972
	37(♂) 36 (♀)	—	44	—	—	—	Senegal	Robbins, in press Matthey and Petter, 1970
	37 (♂) 36 (♀)	—	42	—	—	—	Upper Volta Ghana Ivory Coast	Robbins, in press Matthey and Petter, 1970 Robbins, in press
*Taterillus harringtoni** * (following specimens reported as *T. emini*)							Somalia	
	44	—	—	—	—	1	Ethiopia	Matthey, 1969
	44	—	—	—	—	1	C.A.E.	Genest and Petter, 1973
	44	—	62	—	X:large SM; Y:medium SM	—	Kenya	Robbins, 1973
Taterillus lacustris	28	48	—	18	X:large M; Y:small M	2	Cameroon	Tranier et al., 1974
Taterillus nigeriae	30	—	—	—	—	—	—	Matthey, 1969
Taterillus sp.	18 (♀) 19 (♂)	32–34	26, 28	10, 12	X:large SM; Y:small M	4	Niger	Tranier, 1974*b*
Taterillus pygargus	22–23	40–44	—	—	—	—	Senegal	Matthey, 1969
	23 (♂) 22 (♀)	40–44	—	—	X:large SM; Y_1:small M, Y_2:medium SM	—	—	Petter et al., 1972 Matthey and Jotterand, 1972
Murinae								
Acomys airensis (cahirinus)	42	70	—	28	—	—	Niger	Tranier, 1976*b*
Acomys subspinosus	64	72	—	6	X:large SM	—	South Africa	Matthey, 1965
Aethomys bocagei	50	—	—	—	—	—	—	Matthey, 1963*a*
Aethomys chrysophilus	44	—	—	—	—	—	—	Matthey, 1958
Aethomys granti	32	—	—	—	—	—	—	Matthey, 1964
Aethomys namaquensis	24	—	—	—	—	—	—	Matthey, 1964
Apodemus sylvaticus	48	—	—	—	—	—	—	Matthey, 1936
	48	—	46	0	X&Y:A	—	Europe	Hsu and Benirschke, 4(176), 1970

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Arvicanthis abyssinicus	62	—	—	—	—	—	—	Matthey, 1959
Arvicanthis niloticus	56	—	—	—	—	—	C.A.E.	Matthey, 1965
Cricetomys gambianus	78	—	—	—	X:SM	—	—	Matthey, 1953*c*
Dasymys incomptus rufulus	38	—	—	4	X&Y:A	—	Ivory Coast	Matthey, 1958
Hybomys univittatus	48	—	—	—	—	—	—	Matthey, 1959
Hylomyscus aeta	52	—	—	—	—	—	—	Matthey, 1963*a*
	52	—	—	—	—	2	Fernando Po	Eisentraut, 1969
Hylomyscus alleni	46	—	—	—	—	3	Fernando Po, Cameroon	Eisentraut, 1969
Hylomyscus stella	46	—	—	—	—	—	—	Matthey, 1963*a*
	46	—	—	—	—	4	Fernando Po, Cameroon	Eisentraut, 1969
Lemniscomys barbarus	54	60	—	—	X&Y:M	—	—	Matthey, 1954*c*
Lamniscomys bellieri	56	78	74	10	X:M; Y:M	8	Ivory Coast	Van der Straeten and Verheyen, 1978
Lemniscomys striatus	48	—	—	—	—	—	—	Matthey, 1959
	44	72	68	26	X:M; Y:small M?	15	Ivory Coast	Van der Straeten and Verheyen, 1978
Lophuromys aquilus laticeps	70	—	—	—	—	—	—	Matthey, 1967*a*
Lophuromys flavopunctatus	70	—	—	—	—	—	—	Dieterlen, 1976
Lophuromys s. sikapusi	60	—	—	—	X:SM; Y:M	—	Ivory Coast	Matthey, 1958
Lophuromys woosnomi	42	—	—	—	—	—	—	Dieterlen, 1976
Malacomys edwardsi	48	48	—	0	X&Y:A	—	Ivory Coast	Matthey, 1958
Mastomys erythroleucus	40	—	—	—	X:M; Y:SM	—	Ivory Coast	Matthey, 1958
	38	48–52	—	—	—	—	—	Matthey, 1966*a*, 1965
	38	54	—	—	—	—	Senegal, Morocco	Tranier, 1975
	38	—	—	—	—	—	Zaire	Matthey, 1967*a*
Mastomys natalensis (= *M. coucha*)	36	—	—	—	X&Y:SM	—	South Africa	Matthey, 1954*c* Petter and Genest, 1970
	36	—	44	10	X:large SM; Y:ST	—	—	Hsu and Benirschke, 2(71), 1968
	36	—	—	—	—	—	Rhodesia	Lyons et al., 1977
Mastomys cf. *huberti*	32	—	—	—	—	—	Zaire Senegal	Matthey, 1966*d* Hubert et al., 1973
	32	52	—	—	—	—	Chad C.A.E.	Matthey, 1955 Matthey, 1963*a*
Mus (*Leggada*) *bellus*	30	32	—	—	X:M; Y:A	—	—	Jotterand, 1972
Mus (*Leggada*) *bufo*	36	36	—	—	X:SM; Y:A	—	—	Matthey, 1967*c* Jotterand, 1972

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Mus (Leggada) goundae	16–19	30	—	—	X&Y:M	6	C.A.E.	Jotterand, 1972
Mus (Leggada) haussa	32–34	38	—	—	—	—	Ivory Coast	Matthey, 1967*b* Jotterand, 1972
Mus(Leggada) indutus (deserti)	36	36	—	—	—	—	South Africa	Matthey, 1964*b* Jotterand, 1972
Mus (Leggada) mattheyi	36	36	—	—	—	—	Ivory Coast	Matthey, 1966*c* Jotterand, 1972
	36	36	—	—	—	—	Senegal	Petter et al., 1971
Mus(Leggada) minutoides	32	—	—	—	X:M; Y:SM	—	Ivory Coast	Matthey, 1958
Mus (Leggada) minutoides/ musculoides	18–34	36	—	—	variable	—	—	Jotterand, 1972
Mus (Leggada) oubanguii	28	30–34	—	—	X:M, Y:A	50	C.A.E.	Jotterand 1972
Mus (Leggada) setulosus	36	36	—	—	—	—	Ivory Coast	Matthey, 1964*b* Jotterand, 1972
Mus (Leggada) triton								
Form 1	32	34	—	—	—	—	Zaire	Matthey, 1966*b*
Form 2	20–22	34 (♂) 32 (♀)	—	—	—	—	Tanzania	Matthey, 1963*b*
	—	—	—	—	X:SM; Y:A	—	—	Jotterand, 1972
Mylomys dybowskyi	42	—	—	—	—	—	—	Matthey, 1970
Myomys daltoni	36	—	—	—	—	—	—	Matthey, 1964
Oenomys hypoxanthus	32	—	—	—	—	—	—	Matthey, 1963
Pelomys campanae	48	—	—	—	—	—	—	Matthey, 1963
Praomys hartwigi	34	—	—	—	—	—	Cameroon	Eisentraut, 1968
Praomys jacksoni	28	—	—	—	—	—	—	Matthey, 1958
	28	—	—	—	—	—	C.A.E.	Petter, 1964
Praomys lukolelae	42	—	—	—	—	—	C.A.E.	Matthey, 1970
Praomys morio	42	—	—	—	—	—	C.A.E.	Matthey, 1965
Praomys taitae	48	—	—	—	—	—	—	Matthey, 1965
Praomys tullbergi tullbergi	34	34	—	0	X&Y:A	—	Ivory Coast	Matthey, 1958
Praomys t. minor	34	—	—	—	—	—	C.A.E.	Petter, 1975
Praomys verreauxi	42	—	—	—	—	—	—	Matthey, 1965
Rhabdomys pumilio	48	56	—	8	—	—	South Africa	Matthey, 1954*c*
Thallomys paedulcus	48	—	—	—	—	—	—	Matthey, 1959
Thamnomys surdaster	52	66	62	12	X&Y:SM	—	C.A.E.	Matthey, 1971
	52	66	—	12	X&Y:SM	3	Ivory Coast	Petter and Tranier, 1975
Thamnomys buntingi	52	66	—	12	X&Y:SM	6	Ivory Coast	Petter and Tranier, 1975
Thamnomys gazellae	68–76	—	—	—	X:M	5	C.A.E.	Petter and Tranier, 1976

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Thamnomys rutilans	50	—	—	—	—	—	—	Matthey, 1963
Uranomys ruddi	52	—	—	—	—	—	—	Matthey, 1970
Otomyinae								
Otomys angoniensis pretoriae	56	—	—	—	—	—	South Africa	Matthey, 1964
Otomys unisulcatus	28	—	—	—	—	—	South Africa	Matthey, 1964
Ctenodactylidae								
Ctenodactylus joleaudi	40	—	—	—	—	—	—	Matthey, 1956
Hystricidae								
Hystrix cristata	60	—	—	—	—	—	—	Renzoni, 1967
Rhizomyidae								
Tachyoryctinae								
Tachyoryctes ruandae	48	—	—	—	—	—	—	Matthey, 1967
Tachyoryctes splendens	48	—	—	—	—	—	—	Matthey, 1956
Sciuridae								
Xerus rutilans	38	—	70	34	X:SM; Y:minute M	7	Kenya	Nadler and Hoffmann, 1974
Spalacidae								
Spalax ehrenbergi	60	—	72	14	X:SM; Y:minute	16	Egypt	Lay and Nadler, 1972
Carnivora								
Canidae								
Lycaon pictus	78	—	76	0	X&Y:M	—	—	Wurster and Benirschke, 1968 Hsu and Benirschke, 4(179), 1970
Otocyon megalotis	72	—	—	—	X:SM; Y:small M	—	—	Hsu and Benirschke, 3(122), 1969
Vulpes ruppelli	40	—	—	—	—	—	—	Matthey, 1954*b*
Vulpes vulpes	38	—	—	—	—	—	—	Makino, 1947
	34–38	—	—	—	—	—	Europe	Renzoni and Omodeo, 1972
Felidae								
Acinonyx jubatus	38	—	70	34	X:SM; Y:A	—	—	Hsu et al., 1963 Hsu and Benirschke, 5(234), 1971
Felis aurata	38	—	—	—	—	—	—	Malouf and Schneider, 1965
Felis caracal	38	—	—	—	—	—	—	Hsu and Arrighi, 1966
Felis chaus	38	—	—	—	—	—	—	Manna and Talukdar, 1965

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Felis margarita	38	—	—	—	—	—	—	Jotterand, 1971
Felis nigripes	38	—	70	—	—	—	—	Hsu and Arrighi, 1966
	38	—	68	32	X:M; Y:small M	—	—	Hsu and Benirschke, 2(83), 1968
Felis serval	38	—	68	32	X:M; Y:small SM	—	—	Wurster and Benirschke, 1968 Hsu and Benirschke, 5(235), 1971
Panthera pardus	38	—	68	32	X:medium SM; Y:small ST	—	—	Hsu, 1960 Hsu and Benirschke, 2(84), 1968
Hyaenidae								
Crocuta crocuta	40	—	58	20	X:M; Y:SM	—	—	Wurster and Gray, 1967 Hsu and Benirschke, 2(78), 1968
	—	—	—	—	—	—	South Africa	Wallace and Fairall, 1970
Hyaena brunnea	40	—	70	—	X:SM; Y:A	—	—	Wurster, 1973
Hyaena hyaena	40	—	—	—	—	—	—	Hsu and Arrighi, 1966
Proteles cristatus	40	—	68	30	X:M; Y:small M	—	—	Ulbrich and Schmitt, 1968 Hsu and Benirschke, 3(123), 1969
Viverridae								
Atilax paludinosus	35 (♂) 36 (♀)	—	68	28	X:M; Y:?	—	—	Todd and Pressman, 1967 Hsu and Benirschke, 3(124), 1969
Bdeogale sp.	36	—	68	28	X&Y:SM	—	—	Wurster and Benirschke, 1967*a* Hsu and Benirschke, 5(232), 1971
Bdeogale nigripes	36	—	—	—	—	—	—	Fredga, 1972
Civettictis civetta	38	—	—	—	—	—	—	Todd, 1967
Crossarchus obscurus	36 (♂)	—	—	—	—	—	—	Fredga, 1972
Cynictis penicillata	36	—	—	—	—	—	—	Fredga, 1972
Genetta genetta	54	—	—	—	—	—	—	Matthey, 1965*b*
Genetta genetta neumanni	52	—	92	46	X:SM; Y:A	—	—	Wurster and Benirschke, 1968 Hsu and Benirschke, 3(126), 1969

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Helogale parvula	36	—	—	—	—	—	—	Fredga, 1972
Herpestes ichneumon	48	—	—	—	—	—	—	Wurster and Benirschke, 1968
Herpestes pulverulentus	39 (♂) 40 (♀)	—	—	—	—	—	—	Fredga, 1972
Herpestes sanguineus	41 (♂) 42 (♀)	—	—	—	—	—	—	Fredga, 1972
Ichneumia albicauda	36	—	—	—	—	—	—	Wurster and Benirschke, 1967*a*
Mungos mungo	36	—	—	—	—	—	—	Wurster and Benirschke, 1967*a*
Nandinia binotata	38	—	—	—	—	—	—	Todd, 1967
Suricata suricatta	36	—	68	34	X:SM; Y:T	—	—	Todd, 1966 Hsu and Benirschke, 1(30), 1967
Tubulidentata								
Orycteropidae								
Orycteropus afer	20	—	36	18	X:M; Y:SM	—	—	Benirschke et al., 1970 Hsu and Benirschke, 5(238), 1971
Proboscidea								
Elephantidae								
Loxodonta africana	56	—	58	4	X:SM; Y:A	—	—	Hungerford et al., 1966 Hsu and Benirschke, 6(288), 1971
Hyracoidea								
Procaviidae								
Procavia capensis	54	—	62	10	X:SM; Y:small SM	—	—	Hungerford and Snyder 1969 Hsu and Benirschke, 6(289), 1971
Perissodactyla								
Equidae								
Equus asinus	62	—	98	38	X:SM; Y:A	—	—	Benirschke et al., 1962 Hsu and Benirschke, 1(33), 1967
	62	—	—	—	—			Benirschke and Malouf, 1965

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Equus burchelli antiquorum	44	—	78	36	X:SM; Y:M	2	—	Benirschke and Malouf, 1965
	44	—	—	—	—	—	—	Benirschke et al., 1963
	44	—	—	—	X:M; Y:small M	5	South Africa	Heinichen, 1970
Equus burchelli bohmi	44	—	—	—	—	—	—	Benirschke et al., 1963
Equus burchelli burchelli	44	—	—	—	X:M; Y:small M	4	South W. Africa	Heinichen, 1970
Equus burchelli crawshaii	44	—	—	—	X:M; Y:small M	5	Rhodesia	Heinichen, 1970
Equus grevyi	46	—	76	32	X:M; Y:small M	—	—	Mutton et al., 1964 Hsu and Benirschke, 5(240), 1971
Equus quagga	44	—	76	34	X:M; Y:small A?	—	—	Benirschke and McFeeley, 1963 Hsu and Benirschke, 5(240), 1971
Equus zebra hartmannae	32	—	56	26	X:SM; Y:minute	2	—	Benirschke and Malouf, 1965
	32	—	56	24	X:SM; Y:minute	—	—	Benirschke, 1967 Hsu and Benirschke, 1(37), 1967
	32	—	—	—	—	6	South Africa	Heinichen, 1970
Equus zebra zebra	32	—	—	—	X:large SM; Y:small SM	4	South Africa	Heinichen, 1970
Rhinocerotidae								
Ceratotherium s. simum	84	—	—	—	X:M; Y:A	11	South Africa	Heinichen, 1970
Diceros bicornis	84	—	—	—	—	—	—	Hungerford et al., 1967
	84	—	—	—	X:M	2	South Africa	Heinichen, 1970
Artiodactyla								
Bovidae								
Addax nasomaculatus	58	—	—	—	—	—	—	Wurster and Benirschke, 1968*b*
Aepyceros melampus	58–60	—	—	—	—	—	—	Wallace and Fairall, 1967*a*
	60	—	58	0	X:A; Y:M	—	—	Wurster and Benirschke, 1967*b* Hsu and Benirshcke, 4(188), 1970

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Alcelaphus boselaphus	40	—	—	—	—	—	—	Wurster and Benirschke, 1967*b*
Antidorcas marsupialis	56	—	58	4	X:A; Y:small M	—	—	Wurster and Benirschke, 1967*b* Hsu and Benirschke, 2(89), 1968 Robinson and Skinner, 1976
Ammotragus lervia	58	—	58	2	X:A; Y:small M	—	—	Wurster and Benirschke, 1967*b* Hsu and Benirschke, 3(137), 1969
Capra ibex	60	—	58	0	X:A; Y:small M	—	—	Hauschleck-Jungen and Meili, 1967 Hsu and Benirschke, 3(140), 1969
Cephalophus dorsalis	60	—	—	—	—	—	—	Hard, 1969
Cephalophus grimmi	60	—	—	—	—	—	—	Koulischer et al., 1967
Cephalophus jentinki	60	—	—	—	—	—	—	Hard, 1969
Cephalophus maxwelli	60	—	—	—	—	—	—	Hard, 1969
Cephalophus niger	60	—	—	—	—	—	—	Hard, 1969
Cephalophus rufilatus	60	—	—	—	—	—	—	Hard, 1969
Cephalophus sylvicultor	60	—	58	0	X:SM; Y:A	—	—	Hard, 1969 Hsu and Benirschke, 5(242), 1971
Connochaetes gnou	58	—	58	2	X&Y:A	—	—	Wurster and Benirschke, 1968*b* Hsu and Benirschke, 6(292), 1971
Connochaetes taurinus	58	—	—	—	—	—	—	Wurster and Benirschke, 1968*b*
Damaliscus dorcas	38	—	58	22	X&Y:A	—	—	Wurster and Benirschke, 1967*b* Hsu and Benirschke, 6(293), 1971
Gazella dama	38	—	—	—	—	—	—	Wurster and Benirschke, 1968*b*
Gazella dorcas	31 (♂) 32 (♀)	—	—	—	—	—	—	Wurster, 1972
Gazella gazella	35 (♂) 32 (♀)	—	—	—	—	—	—	Wurster, 1972

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Gazella thomsoni	58	—	60	4	X:medium SM; Y:small M	—	—	Nelson-Rees et al., 1967 Hsu and Benirschke, 2(93), 1968
Hippotragus niger	60	—	58	0	X:large ST; Y:small A	—	—	Wurster and Benirschke, 1968*b* Hsu and Benirschke, 3(142), 1969
Kobus ellipsiprymnus	50	—	—	—	—	—	—	Wurster and Benirschke, 1968*b*
Kobus kob	50	—	58	10	X:A; Y:M	—	—	Taylor et al., 1967 Hsu and Benirschke, 3(143), 1969
Kobus megaceros	52	—	—	—	—	—	—	Wurster and Benirschke, 1968*b*
Oryx gazella	56	—	58	4	X&Y:A	—	—	Hsu and Benirschke, 2(94), 1968
Oryx tao	58 (♀)	—	—	—	—	—	—	Wurster, 1972
Raphicerus campestris	—	—	—	—	—	—	—	Wallace and Fairall, 1967*c*
Syncerus caffer caffer	52	—	58	8	X:large A; Y:small A	—	—	Ulbrich and Fischer, 1967 Hsu and Benirschke, 3(145), 1969
Syncerus caffer nanus	54	—	58	6	X&Y:A	—	—	Wurster and Benirschke, 1967*b* Hsu and Benirschke, 4(192), 1970
Taurotragus oryx	31 (♂) 32 (♀)	—	55–56	26	X:A; Y:A, translocated to an autosome	—	—	Taylor and Taylor, 1970 Hsu and Benirschke, 6(295), 1971
Taurotragus euryceros	33 (♂)	—	—	—	—	—	—	Wurster, 1972
Tragelaphus angasi	55 (♂) 56 (♀)	—	—	2	X&Y:?	—	—	Wurster and Benirschke, 1968*b* Hsu and Benirschke, 6(296), 1971
Tragelaphus scriptus	33(♂) 34(♀)	—	56–58	24–25	X:A; Y:A, translocated to an autosome	—	South Africa	Wallace, 1977
Tragelaphus spekei	30	—	—	—	—	—	—	Wurster et al., 1968
Tragelaphus strepsiceros	31 (♂) 32 (♀)	—	55–56	26	X:A; Y:A, translocated to an autosome	—	—	Wallace and Fairall, 1967*d* Hsu and Benirschke, 6(297), 1971

Appendix I.—Continued.

Taxon	2N	NF	AA	BA	XY morphology	Specimens examined	Country	Citation
Giraffidae								
Giraffa cameleopardis	30	58	54	26	X:large SM; Y:small M	—	—	Wallace and Fairall, 1965
Okapia johnstoni	45	—	—	—	—	—	—	Hösli and Lang, 1970
Suidae								
Phacochoerus aethiopicus	34	—	—	—	—	—	—	Wallace and Fairall, 1967*b*
Sus scrofa	36	—	60	26	X:M; Y:small M	—	—	McFee, 1965 Hsu and Benirschke, 1(39), 1967

PROBLEMS AND PRIORITIES OF RESEARCH ON THE TAXONOMY AND ECOLOGY OF AFRICAN SMALL MAMMALS

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Africa is still one of the research frontiers for studies of small mammal ecology and taxonomy. Yet for specialists from Europe and North America, transportation costs for persons and equipment is expensive and logistical support in Africa is costly. African scientists are not faced with such high expenses to begin or carry on research, but rather have to compete with other priorities in developing countries for funds that might be available for research.

African authorities formulating resource utilization plans are caught between factors of rapidly increasing populations, economic priorities, and potential short-term exploitive policies in attempting to implement long-term integrated land use policies which will allow for and include preservation of various representative ecosystems. Probably the destruction of entire ecosystems in Africa precipitates the greatest concern on the part of specialists studying the ecology and taxonomy of African small mammals. Time is growing critical if studies of many species are to be done adequately. In addition, changes required to insure adequate food supplies and protection from diseases add to the concern. Forest ecosystems, especially relict high forest, are becoming smaller and more isolated. Deserts of Africa are expanding.

Ecological and behavioral studies of small mammals in Africa are hampered by lack of financial support. Most ecological data have been collected opportunistically during other studies. Most population ecology studies are of short duration or seasonal in nature. Long-term monitoring studies of small mammal populations are few in number or include only short periods of trapping during the year. Long-term studies of resource division and habitat utilization have seldom been done. In all instances, quantitative analyses of data are marked by small sample sizes. Sufficient financial support must be made available to allow for long-range studies of up to 10 years' duration. This support must include salaries as well as logistical expenses.

Long-range field studies of behavior are needed for most small mammals. Some of those most obviously offering opportunity for field observations are *Eidolon, Hypsignathus, Thryonomys, Cricetomys, Pedetes,* and various viverrid genera. Recent advances in night vision equipment make it possible to observe many of the nocturnally active genera.

Careful consideration should be given in selecting sites for ecological and behavioral studies. Among those in Africa offering the most pristine environmental conditions are the National Parks and Reserves. These areas, in addition to being more pristine, are staffed by people who have a vested interest in such studies. Laboratory or some other type of sheltered work space is usually available and security for laboratory and field equipment is usually better in these areas than elsewhere.

In most instances, African scientists doing research on small mammals are employed in other roles. Thus, they may only be able to conduct research during their spare time. Whenever possible, these scientists and their students should be included in research projects originating in Europe and North America. Such participation may be the only opportunity for them, especially the students, to learn specialized methodologies and techniques.

In recent years, a more active phase of interest has developed in studies of taxonomy of African small mammals. This upsurge of interest has been precipitated by the need for better taxonomic treatments of various groups of mammals on the part of ecologists, conservationists, agriculturalists, and medical zoologists. Even with the introduction of karyology in taxonomic studies in Africa, methodology still lags far behind some other areas of the world. Commitment of logistical support is needed so that all extant specimens, at least those in the major collections, can be included in taxonomic revisions. There must also be commitments of additional support so that those areas from which critical material is lacking can be visited in order to obtain any necessary missing data. Individuals must be encouraged to use the best and strongest statistical tests available to them in their taxonomic studies. Univariate statistical tests, including analyses of variance, must be a part of any taxonomic study whenever possible. Ideally, multivariate statistical analyses should be included as well. Numerical taxonomic treatments of data in generic and specific revisions of African mammals must be encouraged.

Those individuals who are involved with taxonomic studies of African small mammals are well aware of which groups should be receiving the highest priorities in taxonomic research. However, a review of these groups will indicate the enormous task that remains to be done.

Among the traditional insectivores, one genus stands out in difficulty well above most other African small mammals. The genus *Crocidura* is undoubtedly the most complex of the insectivores and may be of any African mammal (Heim de Balsac and Meester, 1977). Sibling species are common, often sympatric in distribution, and study specimens are usually inadequate in number and widely distributed. Heim de Balsac and Meester (1977) list 85 species, but admit that this is a tentative compilation. Other insectivores deserving of treatment are the hedgehogs and golden moles at both generic and specific levels. Recent taxonomic arrangements of the latter by Simonetta (1968) and Meester (1974) indicate the differences of opinion that exist on the number and relationships of genera and species. Other genera, such as *Myosorex, Sylvisorex, Suncus,* and *Elephantulus* are deserving of additional attention but less critically so at this time.

Within the bats, a large number of genera are in critical need of taxonomic revision. Chief among these are *Epomops, Epomophorus, Rousettus, Taphozous, Rhinolophus, Hipposideros, Myotis, Nycticeius (sensu lato), Pipistrellus, Eptesicus, Scotophilus, Glauconycteris (sensu stricto), Kerivoula, Miniopterus,* and *Tadarida*. Some genera, such as *Rousettus, Pteropus, Emballonura, Plecotus, Nyctalus, Miniopterus,* and *Otomops,* have major Eurasian affinities as well, and taxonomic studies of these genera must consider both continents. Others, such as *Rhinolophus, Hipposideros, Pipistrellus, Eptesicus* and *Tadarida,* seem to separate into species groups on a continental basis.

The genus *Lepus* is in critical need of taxonomic treatment over the whole of Africa and Eurasia. In addition, a monographic study of both Recent and fossil genera of lagomorphs, including all continents of occurrence, should be encouraged.

The group showing the highest radiation of species in Africa is the rodents. Within this group, the squirrels contain the genera *Funisciurus* and *Paraxerus,* which are critically in need of taxonomic revisions. Additionally, *Heliosciurus* is deserving of attention, with both *H. rufobrachium* and *H. gambianus* in need of studies of geographic variation. Studies of generic relationships are needed for both sciurid and anomalurid squirrels.

Among the genera of small rodents, the following African ones are in critical need of taxonomic revisions, utilizing every available method of establishing specific relationships: *Meriones, Gerbillus, Tatera, Taterillus, Gerbillurus, Mus, Aethomys, Acomys, Arvicanthis, Hybomys, Lemniscomys, Lophuromys, Pelomys, Mastomys, Praomys (sensu stricto), Hylomyscus, Grammomys, Cryptomys, Tachyoryctes, Steatomys, Dendromus, Otomys,* and *Graphiurus*. Attempts should be made to include in these studies other data than those traditionally included, for example, differences in life history, morphology of glans penes, sperm morphology, and karyotypes.

Additionally, studies of geographic and non-geographic variation are required for a number of currently recognized monotypic genera and some genera with only a few species. Without doubt, Ellerman (1940, 1941) and Ellerman et al. (1953) oversynonomyzed certain genera of rodents. Hubert (1978) has shown good evidence for two species in the genus *Saccostomus*. Other monotypic genera, which should receive critical review of geographic variation are *Dasymys, Oenomys, Rhabdomys, Thallomys, Uranomys, Malacothrix, Pedetes, Desmodillus,* and *Psammomys*.

Unfortunately, in many taxonomic revisions of African genera of rodents published in the past, insufficient attention has been given to non-geographic variation. Secondary sexual and age variation are present in nearly all rodents. Care must be exercised to compare only rodents of the same age in these taxonomic studies as these animals invariably continue to grow throughout most of their life.

In the remaining groups of small mammals, taxonomic studies are needed at the generic and specific levels for the prosimians, particularly *Galago,* the viverrids, especially *Genetta,* and the antelope genera *Cephalophus (sensu lato), Madoqua,* and *Gazella*. Hoeck (1978) has introduced a new approach in the study of the generic relationships of hyraxes and indicates as well the need for a comprehensive study of the genus *Procavia*.

Until better taxonomic treatments of many genera are available, statistical studies of the zoogeographic relationships of African mammals on a continental basis will be inadequate. Unfortunately, many zoogeographical studies, even regional ones, must make concessions for areas lacking adequate faunal surveys and for taxonomic confusion in certain genera.

Faunal surveys of African countries are becoming less common, primarily due to difficulties in obtaining necessary funding for such field work and maintenance of resulting collections. Yet, nonmammalogists are voicing an increasing desire for reports of the mammals of a given country. Even so, mammal surveys of certain regions would still be a valuable undertaking. The Ogoue Basin, the central Sahara, the western Sahara in the region formerly included in Spanish Sahara, the horn of Africa including Somalia, Ethiopia, and particularly Eritrea Province, the massifs on either side of the Rift in Central Africa, southern Zaire, and eastern Angola are in need of additional surveys for mammals.

Attention to endangered species of African mammals has focused mainly on large mammals and the primates. Many species of small mammals are so poorly known it is impossible to judge their status. Many obviously good species are known by less than 12 specimens, for example, *Leimacomys buttneri, Dendroprionomys rousseloti, Zinkerella insignis, Hylomyscus baeri,* and *Glauconycteris superba*.

Permits to conduct ecological and taxonomic studies in Africa are not required in all countries. Before issuing permits, some others require a complete and detailed proposal of the research to be submitted well in advance of the starting date; Kenya, for example, requires this information six months in advance. Without such permission, research conducted in these countries is illegal. For most countries, export of specimens requires a special permit or at least a letter of waiver. Unless all of the specialists cooperate in obtaining the necessary permission to conduct research and subsequent permits, requirements will become more restrictive and permission more difficult to obtain.

Individuals performing any type of research in Africa are well aware of the problems associated with economic growth versus conservation efforts. In dealing with the problems in this regard, the nations of Africa, although almost all are in a developing state, are no different from those of Europe and North America. However, the participants of the colloquium felt they would be remiss in their professional responsibility if they did not consider the destruction of various habitats, particularly forest ecosystems, and the mammals occurring there. The recommendations below received unanimous approval from the participants.

RECOMMENDATIONS OF THE PARTICIPANTS IN THE COLLOQUIUM ON ECOLOGY AND TAXONOMY OF AFRICAN SMALL MAMMALS SPONSORED BY CARNEGIE MUSEUM OF NATURAL HISTORY, 19–22 SEPTEMBER 1977

I. The participants of the Colloquium on Ecology and Taxonomy of African Small Mammals recognize that these animals play an important ecological role in many natural and man-made habitats. Some species can be pests of agriculture and forestry as well as disease vectors in many parts of the continent. The Colloquium fully recognizes the high priority to be given to these problems.

II. However, all of these species are vital to the functioning and maintenance of natural ecosystems. Furthermore, the role of many is totally unknown although probably very important in most instances. In view of the rapid decimation of natural habitats in Africa, particularly all types of natural forests, due to human encroachment and development of exotic tree plantations, the participants of the Colloquium on Ecology and Taxonomy recommend that Institutions of all African countries and the International agencies concerned with these countries:

  A. Make every possible effort to conserve large and representative examples of all mature forest types, particularly montane and rain forests, which exist within their respective countries or areas of interest. These forest parks or nature reserves must be large enough (circa. 2,000 square km) to conserve viable populations of all animals and plants comprising the ecosystem, and must be completely protected against all forms of destructive exploitation. In some circumstances the remaining relict forest blocks are much smaller than the recommended size and in these cases an area as large as possible should be conserved. Where possible, boundaries of existing forest parks and nature reserves should be expanded to include sufficiently large and representative areas;

B. Make every possible effort to develop educational programs in their schools and mass media for their general public which explain the value and necessity of forest conservation, and the importance of land-use programs based on long-term ecological goals rather than short-term exploitation;

C. Make every possible effort to develop integrated land-utilization policies based on sound scientific and long-term ecological principles, to overcome the competitive nature which usually prevails in the interactions of the various government departments concerned with land-utilization problems;

D. Make every possible effort to have all proposals for land, agricultural, and industrial development schemes reviewed by a board of ecologists before these proposals are implemented;

E. Encourage basic and long-term biological research on forest ecosystems. This research should include not only projects of theoretical importance, but those of relevance to the practical problems in the countries concerned, such as the control of pest species through the conservation of natural and mature forest habitats.

III. The participants further concurred that integrated land-use policies based on long-term interests provide a more sound economic base than the short-term exploitive policies currently prevailing in many countries.

IV. Finally, and of primary importance, it was recognized that many of the problems associated with the implementation of these recommendations are directly related to the human population explosion.

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